# ECOLOGY

VOL. 34 JULY, 1953 No. 3

## FOREST COMPOSITION AND SPECIES ASSOCIATION IN THE BEECH-MAPLE FOREST REGION OF WESTERN OHIO[1]

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Witness trees from the land survey records have proved useful as indices of the character of the original vegetation and have served as a primary basis (Sears 1925; Kenoyer 1930, 1940; Blewett and Potzger 1950; Rohr and Potzger 1950; Potzger and Potzger 1950) or as a confirmatory or supplementary source of information (Lutz 1930; Crowl 1937; Dobbins 1937; Shanks 1937, 1938; Gordon 1940; Fassett 1944; Cottam 1949; Norris 1949) in a number of vegetation surveys in Ohio, Michigan, Indiana, Pennsylvania, New York, and Wisconsin.

The present study is based on the land survey records for Shelby County, Ohio, a typical sample area in the heart of the beech-maple forest region of western Ohio (Transeau and Sampson 1935; Braun 1950). Its objectives are: (1) species composition of the original forest based on the witness trees as a representative sample of the vegetation; (2) forest composition differences with differences in soil type and relief; (3) changes in species composition in the secondary forest; (4) analysis of the degree of association between the species used as witness trees in the original land surveys, based on the random pairs of trees used as witnesses at section and quarter-section corners; and (5) inferences as to habitat range of major species and their role in the forests.

The original land surveys of Shelby County were made by nine surveyors during the years 1798-1832. The typical congressional land survey procedure was used, the land being divided by a grid into sections one mile square. Survey points were established at section corners and at intervening half-mile intervals (quarter-section corners) on alternate survey lines. Thus, each mile-square section had six survey points touching it, but the over-all average was two points per square mile, involving four witness trees per square mile. With the addition of survey corners along the river and county lines, 2030 trees were listed for this sample area of approximately 413 square miles. These witness tree records were transcribed onto topographic maps for certified copies of the survey records in the County Courthouse, Sidney, Ohio.

Several assumptions underlie the analyses and conclusions of this paper: (1) that the species names in the survey records are consistent and identifiable; (2) that the samples are large enough to have validity; (3) that the witness trees are random pairs; and (4) that species can be used as habitat indices. The first two of these assumptions have commonly been discussed in papers which have justified the use of witness trees as a basis of vegetation inferences (Sears 1925;

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 146. Review of the manuscript and suggestions concerning soil interpretation and terminology by W. S. Ligon, Principal Soil Scientist, Division of Soil Survey, U. S. Dept. of Agriculture, are gratefully acknowledged.

Shanks 1937, 1938; Crowl 1937). The last two assumptions relate in particular to the present investigation. All will be discussed in turn.

### Species Identification

The importance of witness trees as reference points made correct identification of species a basic requirement of the pioneer land surveyor. Vernacular names were employed consistently and correspond with those now in use in the area. Their interpretation is based on the writer's field experience in western and northern Ohio, including field work in Shelby County during the summer of 1938 as Agent on Barberry Eradication for the U. S. Department of Agriculture. The inclusion of a number of relatively rare and economically unimportant species, such as blue ash, red ash, white walnut, buckeye, willow, aspen, sassafras, mulberry, dogwood, redbud and water beech, is evidence of the surveyors' ability to distinguish and identify the trees of the region. Unfortunately, the species of hickory were not distinguished. It is likely that most of the hickory references were to *Carya ovata* (Mill.) K. Koch, but *C. cordiformis* (Wang.) K. Koch, though less common, was also widely distributed on moist to intermediate sites, and it is possible that occasional trees of *C. glabra* (Mill.) Sweet or *C. tomentosa* Nutt. were encountered in areas of oak dominance.

The following list of 35 species or species groups recognized in the land surveys includes all but one (cottonwood, *Populus deltoides* Marsh.) of the species listed in the Ohio Forest Survey report a century later (Root 1941). The 20 species common to both lists are indicated by asterisks. Scientific names follow Gray's Manual of Botany, eighth edition (Fernald 1950).

| | |
|---|---|
| white oak | **Quercus alba* L. |
| black oak | *Q. velutina* Lam. |
| red oak | **Q. rubra* L. (possibly including *Q. shumardii* Buckl.) |
| swamp oak, bottom oak | *Q. bicolor* Willd. |
| bur oak | *Q. macrocarpa* Michx. |
| pigeon oak | *Q. muehlenbergii* Engelm. (?) |
| hickory | **Carya* spp. |
| beech | **Fagus grandifolia* Ehrh. |
| sugar (sugar maple) | **Acer saccharum* Marsh. (including some *A. nigrum* Michx. f.) |
| maple (silver maple) | **A. saccharinum* L. |
| box elder | **A. negundo* L. |
| white ash, ash | **Fraxinus americana* L. |
| black ash, swamp ash | **F. nigra* Marsh. |
| blue ash | *F. quadrangulata* Michx. |
| red ash | *F. pennsylvanica* Marsh. |
| elm, white elm | **Ulmus americana* L. (probably including *U. thomasi* Sarg.) |
| red elm (slippery elm) | *U. rubra* Muhl. |
| walnut (black walnut) | **Juglans nigra* L. |
| white walnut | *J. cinerea* L. |
| cherry | **Prunus serotina* Ehrh. |
| buckeye | *Aesculus glabra* Willd. |
| lynn (basswood) | **Tilia americana* L. |
| willow | **Salix nigra* Marsh. |

| | |
|---|---|
| aspen | *Populus tremuloides* Michx. |
| locust | **Gleditsia triacanthos* L. |
| ironwood, hornbeam | **Ostrya virginiana* (Mill.) K. Koch |
| sassafras | *Sassafras albidum* (Nutt.) Nees |
| poplar | **Liriodendron tulipifera* L. |
| haw bush, thorn, white thorn | **Crataegus* spp. |
| mulberry | *Morus rubra* L. |
| dogwood | *Cornus florida* L. |
| redbud | *Cercis canadensis* L. |
| water beech | *Carpinus caroliniana* Walt. |
| sycamore | **Platanus occidentalis* L. |
| hackberry | **Celtis occidentalis* L. |

### Size and Validity of Sample

The witness trees constitute an extremely small sample of the vegetation, averaging only five trees per square mile; only about a dozen trees are listed along the edges of each mile-square section. Only in the case of extremely homogeneous vegetation could such a sample yield useful direct information with respect to the distribution or composition of specific vegetation types, and it is obvious that with decrease in homogeneity of the vegetation the reliability of this small sample as a basis for detailed mapping would decrease rapidly.

It therefore becomes advisable to use land survey records only as contributory evidence in detailed vegetation mapping. Field studies of remnants of natural vegetation to establish mapping types, to determine their topographic correlation, and to distinguish their indicator species, must form the primary basis. The use of land survey records in detailed mapping is best restricted to topographic interpretation of spot records of the presence of indicator species.

However, broad generalizations as to regional composition of the original vegetation may be safely based on the land survey records (Sears 1925, Kenoyer 1940, Potzger and Potzger 1950) and generalized vegetation maps may in turn be based on them (*e.g.*, Figure 12, facing page 354, *Naturalist's Guide to the Americas* (Shelford 1926), based on Sears' data). It is toward such broad generalizations regarding regional forest composition in the beech-maple forest region that the percentage analyses of the present study are directed. There is no evidence that the surveyors selected certain species as witness trees, and the witness trees at prescribed intervals along directional survey lines are considered to constitute an unbiased sample of the vegetation and a sound basis for composition inferences.

### Witness Trees as Random Pairs

It has been pointed out (Cottam and Curtis 1949) that random pairs of trees may serve as very efficient samples of the arborescent layer of forest vegetation, and this sampling method has been applied to an extensive survey of Wisconsin forest remnants (Curtis and McIntosh 1951). The typical land survey listing of witness trees in pairs without species selection, at predetermined points on the survey grid, amounts to similar random pair sampling, and provides an unbiased basis for an estimate of the degree of association between the species participating in the vegetation. The witness trees (usually two) at a survey corner are considered to be a random sample of the trees associated in the same habitat or contiguous habitats. The land survey records thus yield information on organization as well as composition of the original forests.

### Species as Habitat Indices

A fundamental postulate of plant geography, formally expressed in Good's

(1947) Theory of Tolerance, is the principle that each plant species has its potential area or habitat range, genetically based, beyond which it is incapable of reproduction. This, together with its corollary that there is a modal point or optimum within the habitat range of a species, is the principle which underlies the use of plants as "indicators" of environment (A. W. Sampson 1939), and which provides the basis for such inductive approaches to the description and classification of vegetation as those of H. C. Sampson (1930), Curtis and McIntosh (1951), and Whittaker (1948, 1951). This is likewise the orienting principle in the analysis of species association in the present study, which leads to generalizations regarding habitat range of species through the use of associated species as habitat indices.

## Forest Composition

The primary importance of beech in the original forests is illustrated in Table I, which also indicates that for the county in general sugar maple, usually regarded as the characteristic associate of beech (Shantz and Zon 1924, Sampson 1927, Weaver and Clements 1938, Gordon 1932, Braun 1950), is so much lower in abundance that it can scarcely be said to share regional dominance. Without prejudice, one would be led to generalize the original vegetation of Shelby County as *beech* forest rather than *beech-maple* forest. This generalization obviously applies to a composite of the entire vegetation complex of the area, which included oak-hickory and swamp forest types and transitions between them and the climax beech and beech-maple types (Sampson 1930, Transeau and Sampson 1935, Root 1941, Braun 1950), and implies that beech, which made up 42% of the total trees listed, must have been decidedly predominant in the types in which it occurred.

Table I. *Percentage composition of original forests and forest remnants of Shelby County*

| Species | Original forests 1796-1832 | | | | Forest remnants 1939 |
|---|---|---|---|---|---|
| | Entire county | Gray-brown podzolic soils | Gray-brown podzolic intergrades | Humic gley soils | |
| Beech | 42.0 | 45.1 | 43.1 | 24.9 | 2.7 |
| Hickory | 9.8 | 9.8 | 9.2 | 10.9 | 18.0 |
| White oak | 8.6 | 6.6 | 12.8 | 12.1 | 9.1 |
| White ash | 8.4 | 7.7 | 10.4 | 9.1 | 11.6 |
| Sugar maple | 7.4 | 9.1 | 4.3 | 4.1 | 8.5 |
| Elm | 7.4 | 5.8 | 6.4 | 17.0 | 24.0 |
| Red oak | 2.7 | 2.5 | 1.9 | 4.9 | 6.2 |
| Basswood | 2.0 | 1.9 | 2.1 | 2.6 | 3.5 |
| Black walnut | 0.5 | 0.4 | 1.2 | 0.4 | 2.5 |
| All others | 11.2 | 11.1 | 8.6 | 14.0 | 13.9 |
| Total | 100.0 | 100.0 | 100.0 | 100.0 | 100.0 |
| No. trees in sample | 2030 | 1339 | 422 | 269 | >150,000 |

Evidence on this point and on forest type differentiation is presented in the soil group generalizations in Table I and in Table II, which summarizes forest composition in each of the soil type association areas of the generalized soil map of Conrey (1945). It must be remembered that this is not a detailed soil survey, but that the areas are delimited in terms of predominant and characteristic soil types. Thus, areas mapped as Miami silty clay loam usually include relatively small and discontinuous areas of the poorer drained Crosby and Brookston soils, and areas mapped as types of Brookston or Clyde are likely to include spots of better drained soils. As Table II shows, some of the samples are quite small. Larger samples are obtained in Table I by combining those from soils of similar catena position and profile character. The Bellefontaine and Miami types are generalized as zonal (normal profile) soils (Catena positions 5-4) of the Gray-Brown Podzolic great soil group; the Crosby types are Gray-Brown Podzolic intergrades (Catena position 2); and the Brookston silty clay loam and Clyde silty clay loam are Humic Gley soils (Catena positions 8-9) and are

TABLE II. *Percentage analysis of original forest composition by soil type association areas*

| Soil area | Bellefontaine silt loam | Miami silt loam | Miami silty clay loam, slope phase | Miami silty clay loam | Crosby silt loam | Crosby silty clay loam | Brookston silty clay loam | Clyde silty clay loam |
|---|---|---|---|---|---|---|---|---|
| No. trees in sample | 26 | 195 | 276 | 842 | 81 | 341 | 225 | 40 |
| Species attaining over 5% | | | | | | | | |
| White oak | 7.7 | 1.5 | 6.2 | 7.8 | 4.9 | 14.7 | 10.7 | 20.2 |
| Red oak | ... | 1.0 | 1.1 | 3.3 | ... | 2.3 | 3.6 | 12.5 |
| Hickory | 15.4 | 4.1 | 4.7 | 12.6 | 4.9 | 10.3 | 11.6 | 7.5 |
| Sugar maple | 11.5 | 11.3 | 16.7 | 6.1 | 6.2 | 3.8 | 4.0 | 5.0 |
| Beech | 42.3 | 56.5 | 42.0 | 43.6 | 46.9 | 42.2 | 26.2 | 17.5 |
| Basswood | ... | 1.5 | 1.8 | 2.0 | 8.6 | 0.6 | 3.1 | ... |
| White ash | 19.2 | 7.7 | 4.0 | 8.6 | 7.4 | 11.2 | 8.4 | 12.5 |
| Elm | ... | 4.6 | 4.7 | 6.7 | 8.6 | 5.9 | 16.9 | 17.5 |
| Species attaining 1 to 5% | | | | | | | | |
| Black ash | ... | 2.6 | 1.8 | 0.8 | 4.9 | 0.6 | 2.7 | ... |
| Buckeye | ... | 1.5 | 4.7 | 1.1 | ... | 1.5 | ... | ... |
| Water beech | 3.8 | ... | 1.4 | 0.5 | ... | ... | 0.9 | ... |
| Hop hornbeam | ... | 1.0 | 0.7 | 0.8 | 3.7 | 1.2 | 0.4 | ... |
| Silver maple | ... | ... | 0.4 | 1.0 | 2.5 | 1.8 | 3.6 | 2.5 |
| Blue ash | ... | 3.1 | 2.9 | 0.6 | 1.2 | 1.5 | 1.3 | ... |
| Black walnut | ... | 0.5 | 0.7 | 0.2 | ... | 1.5 | ... | 2.5 |
| Honey locust | ... | ... | 0.7 | ... | ... | ... | 1.3 | 2.5 |
| Black oak | ... | ... | 0.4 | 1.5 | ... | ... | 1.8 | ... |
| Tulip poplar | ... | 1.5 | ... | 0.1 | ... | ... | ... | ... |
| Willow | ... | ... | ... | ... | ... | ... | 1.3 | ... |
| Sycamore | ... | ... | 1.1 | ... | ... | ... | ... | ... |

grouped together (Bushnell 1944; Thorp and Smith 1949).

An examination of Tables I and II indicates that the best expression of the beech-maple association occurred in the Miami silt loam area (east and south of the Great Miami River) with 67.8% of the trees belonging to these two species. In the heavier-textured Miami silty clay loam area, the abundance of these two species was only 49.7%. The abundance of sugar maple decreased more than that of beech with this change in soil texture. A similar decrease in abundance of both species occurred from the Miami to the Crosby series in each texture class (silt loam and silty clay loam), with sugar maple decreasing more than beech in both

cases. It seems that decrease in soil aeration, whether it results from heavier soil texture or from poorer surface and internal drainage due to topographic position, is more unfavorable to sugar maple than to beech. The relative habitat range of these two species may be checked in the other direction by going from the area of Miami silty clay loam, the typical and extensive upland soil of central Shelby County, to the area of the same soil type, slope phase, which characterizes the rolling to broken topography along the Great Miami River and its major tributaries. This topographic change is marked by a shift to good beech-maple dominance, with sugar maple increasing to its maximum abundance of 16.7%, while beech does not increase at all.

The distribution of white oak, red oak, and elm is complementary to that of beech and sugar maple. These five species together made up 61.4 to 72.7% of the sample in the various soil areas. The oaks and elm are also potential dominants, and are characteristically abundant in habitats where competition from beech and sugar maple is absent or less pronounced. Although the modal point in habitat range of white oak lies on the dry side of beech and sugar maple, it would appear from these data that its range of tolerance of heavier soil texture and decreased soil aeration exceeded theirs.

The last column of Table I summarizes the species composition of the forest remnants of Shelby County a little more than a century after the last of the original land surveys were completed (Root 1941). By the time of the 1939 Ohio Forest Survey only 6.7% of the area of Shelby County was occupied by woodlands. A cruise covering 7.9% of this wooded portion provided the basis of the percentage estimates. Selective clearing of the better agricultural land had left a relatively high representation of habitats originally swampy. This is reflected in the closer resemblance of forest remnant composition to original composition on the humic and low humic gley soil areas than on either of the other generalized soil areas. Selective cutting, pasturing, and artificial drainage had opened the canopy and understory and altered the habitat conditions. Elm, white ash, and sugar maple were reproducing abundantly and a trend toward a secondary forest type numerically dominated by these three species was indicated. Such a type already occupied 34.9% of the woodlot area. Little evidence of the original upland dominance of beech remained. It had dropped from first place to eighth. Scarcely enough beech or beech-maple forest remained to establish their site correlation.

## Species Association

Since the vegetational association concept rests ultimately on the association between individual plants, it has seemed worthwhile to measure the degree of association between species in the random pairs of witness trees in the present sample.

All combinations of individual trees were tabulated. In the relatively few cases where more than two trees were listed, each combination of two individuals was used. This provided more than a thousand combinations in which beech participated, and more than 200 each for hickory, white oak, and white ash, with elm and sugar maple not far behind (Table III). Minor species not listed in Table III were so infrequent that the small samples of their combinations are highly erratic and no reliable basis for inferences concerning their degree of association is provided. This is illustrated by the absence of the red oak-basswood combination from Table III. The probability of this combination would be estimated as .00054, if these species were distributed independently and at random, or less than one such pair in the entire county sample, so its absence is not surprising.

TABLE III. *Analysis of combinations with major species among the random pairs of witness trees*

| | White oak | | Red oak | | Hickory | | Sugar maple | | Beech | | Basswood | | White ash | | Elm | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % |
| White oak | 62 | 28.2 | 14 | 19.7 | 19 | 7.4 | 8 | 4.7 | 55 | 5.4 | 2 | 4.8 | 24 | 11.4 | 17 | 9.5 |
| Red oak | 14 | 6.4 | 4 | 5.6 | 9 | 3.5 | 4 | 2.4 | 23 | 2.2 | .. | .... | 5 | 2.4 | 5 | 2.8 |
| Hickory | 19 | 8.6 | 10 | 14.1 | 40 | 15.7 | 11 | 6.5 | 97 | 9.5 | 7 | 16.7 | 26 | 12.3 | 21 | 11.7 |
| Sugar maple | 8 | 3.6 | 4 | 5.6 | 11 | 4.3 | 50 | 29.4 | 68 | 6.7 | 4 | 9.5 | 10 | 4.7 | 2 | 1.1 |
| Beech | 55 | 25.0 | 23 | 32.4 | 97 | 38.1 | 68 | 40.0 | 596 | 58.5 | 14 | 33.3 | 52 | 24.7 | 26 | 14.5 |
| Basswood | 2 | 0.9 | .. | .... | 7 | 2.7 | 4 | 2.4 | 14 | 1.4 | 2 | 4.8 | 9 | 4.3 | 2 | 1.1 |
| White ash | 24 | 10.9 | 5 | 7.0 | 26 | 10.4 | 10 | 5.9 | 52 | 5.1 | 9 | 21.4 | 44 | 20.9 | 18 | 10.1 |
| Elm | 17 | 7.7 | 5 | 7.0 | 21 | 8.2 | 2 | 1.2 | 26 | 2.6 | 2 | 4.8 | 18 | 8.5 | 48 | 26.8 |
| All others | 19 | 8.6 | 6 | 8.5 | 25 | 9.8 | 13 | 7.6 | 88 | 8.6 | 2 | 4.8 | 23 | 10.9 | 40 | 22.4 |
| Totals | 220 | | 71 | | 255 | | 170 | | 1019 | | 42 | | 211 | | 179 | |

Each of the columns in Table III is an analysis of the associates of a particular species in the Shelby County sample. It may be noted that 58.5% of the associates of beech were also beech trees, and that beech was likewise the most frequent associate of all the other major species except white oak and elm. These facts emphasize its role as a forest dominant in the region. But of even more interest is the relative degree of association of each of the other major species with it, a relationship which can be measured by comparing the percentage analysis of its associates with the percentage composition of the forest sample for the entire county (first column of Table I). The resulting ratios of actual occurrence to random expectation are listed in Table IV for the combinations of the major species with each other, and provide the basis for the graphic summary of Figure 1. Basswood has been omitted from the graphs in order to limit them in existing combinations, and the principal value of its inclusion in Table IV is to illustrate the erratic variation in a small sample.

These data provide quantitative support for the conventional association-inferences and bear testimony to the reality of certain kinds of association. A well-developed beech forest type in which sugar maple is relatively unimportant is indicated. The importance of such a type

TABLE IV. *Ratios of actual occurrence of species in random pairs to random expectation based on entire county sample (data of columns of Table III/data in first column of Table I)*

| | White oak | Red oak | Hickory | Sugar maple | Beech | Basswood | White ash | Elm |
|---|---|---|---|---|---|---|---|---|
| White oak | *3.3* | 2.3 | 0.9 | 0.5 | 0.6 | 0.6 | 1.3 | 1.1 |
| Red oak | 2.4 | *2.1* | 1.3 | 0.9 | 0.8 | ... | 0.9 | 1.0 |
| Hickory | 0.9 | 1.4 | *1.6* | 0.7 | 1.0 | 1.7 | 1.3 | 1.2 |
| Sugar maple | 0.5 | 0.8 | 0.6 | *4.0* | 0.9 | 1.3 | 0.6 | 0.1 |
| Beech | 0.6 | 0.8 | 0.9 | 1.0 | *1.4* | 0.8 | 0.6 | 0.3 |
| Basswood | 0.5 | ... | 1.4 | 1.2 | 0.7 | *2.4* | 2.2 | 0.6 |
| White ash | 1.0 | 0.9 | 1.1 | 0.8 | 0.7 | 2.9 | *2.8* | 1.4 |
| Elm | 0.7 | 0.7 | 0.8 | 0.6 | 0.2 | 0.4 | 0.9 | *1.9* |

is attested by the fact that pairs of beech trees make up 27.5% of the total witness tree combinations. The tendency toward exclusiveness of sugar maple and beech, presumably due to their heavy and tight canopy closure, is illustrated. All the other major species except hickory fall below random expectation in their vicinity. The segregation of an oak-hickory type is supported by the high ratios among its species-combinations and the relatively low degree of association of beech and sugar maple with the species of oak and hickory. The decrease of beech and sugar maple at the other end of the moisture scale, in association with elm, is quite pronounced. Phases of the elm-ash-soft maple swamp forest described by Sampson (1930) are indicated in this habitat range, here characterized by great variability in forest composition, by relatively high representation of elm and ash and low representation of maple.

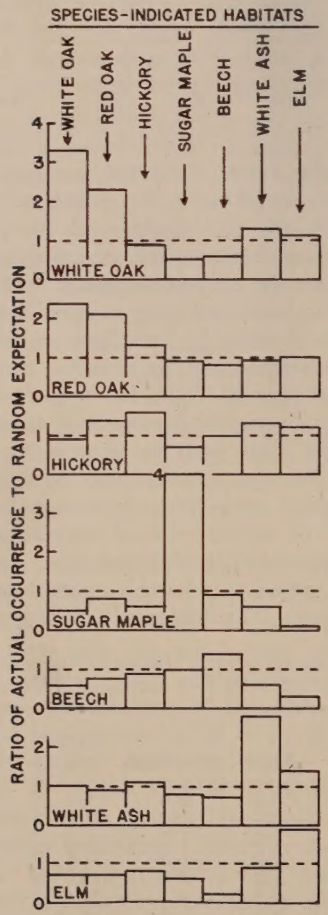


FIG. 1. Graphic representation of habitat ranges of major species in terms of their association with indicator species in random pairs.

## HABITAT RANGES

Each graph in Figure 1 represents the distribution of a species (or species group) in a series of habitats defined by its associated species. These species-indicated habitats are arranged along a moisture gradient, with sugar maple and beech defining the most mesic range, hickory and the oaks indicating the drier range to the left, and white ash and elm indicating the wetter range to the right. This order of arrangement is based on field observations in the area, and is supported by the data of Table II, by the habitat inferences of Sampson (1930), and by the smoothness of the implied distribution curves in Figure 1. The height of each bar in the histograms is determined by the ratio of actual occurrence to random expectation in that habitat, the reference line representing a ratio of one. Thus, bars below the line represent values below the average for the county and bars extending above the line represent points of concentration for the species.

It is not surprising that in every graph except one (red oak), the greatest over-representation of a species is in its self-defined habitat, indicating *contiguous distribution* ("contagious" distribution in the sense of Cole [1946]) in excess of inter-species association. These examples illustrate the concept of (positive) contiguous distribution, the tendency of the individuals of a species to become concentrated in excess of random expectation. The height of bar above the reference line is in each of these cases indicative of the degree of contiguous distribution. These ratios cannot be fairly compared, however, for even if beech oc-

curred with beech in every case, the ratio of actual occurrence to random expectation would be only 1.00/.42 = 2.38, while sugar maple with its lower average abundance had an actual ratio of 4.0. A more reasonable comparison is illustrated in Figure 2, in which contiguous distribution ($C$) may be visually compared with the space available for such increase ($100\%-R$). A mathematical comparison of these values may be used as an index of contiguous distribution:

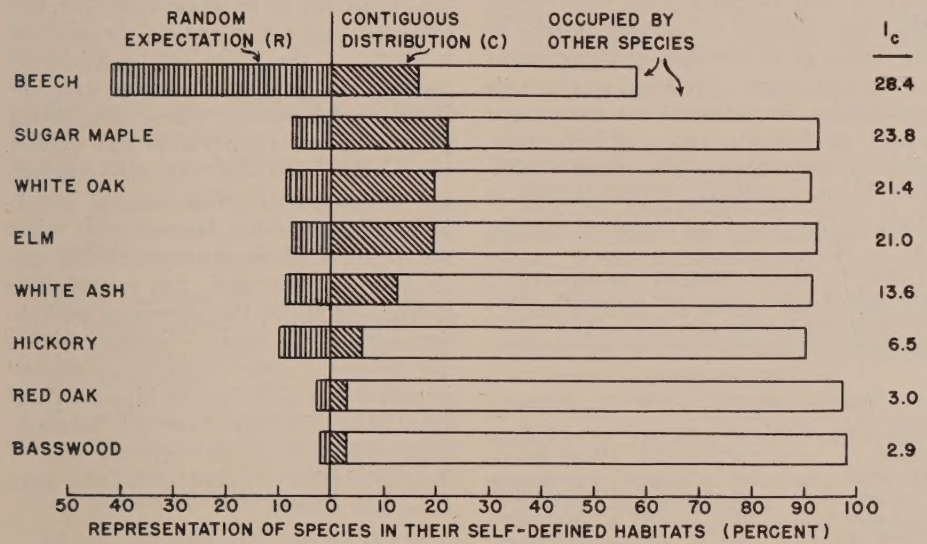


FIG. 2. Analysis of contiguous distribution in terms of degree of self-association of species in random pairs.

$A$ = actual abundance in subsample (%);
$R$ = random expectation based on county total (%);
$A-R = C$, contiguous distribution (%);
$\frac{A-R}{100-R} = \frac{C}{100-R} = I_c$, index of contiguous distribution (%).

Values of this index are listed at the right margin of Figure 2, and lie between 20 and 30% for the species which are major dominants, providing a reasonable quantitative measure of species concentration. Values of this index are positive when $A$ exceeds $R$, and could theoretically reach a maximum of 100% if a species ever occurred only in exclusive pure stands.

It is apparent that in this sample, each major species shares a part of its habitat range with each other major species, and it is useful to think of the forests as a *continuum* in the sense of Curtis and McIntosh (1951) in which the habitats as well as the forest stands might be arranged in a virtually continuous series along some selected gradient. When this is done and species distribution along that gradient is plotted, an approximation of a normal distribution curve or portion of one is obtained. In the first two cases in Figure 1, white oak and red oak, the modal point of the curve lies at or beyond the dry edge of the graph. That of elm lies at or beyond the wet edge. Both sugar maple and beech reach their peak in the mesic range and taper in both directions, representing more adequately the complete pattern of species distribution. Hickory and white ash would apparently yield similar curves if it were

not for their marked depression in the vicinity of sugar maple and beech.

Since the associated species in Table IV increase in abundance in both directions from the sugar maple and beech habitats, this mesic range is obviously a part of their potential area, from which they are excluded in varying degree by the influence of the tight-canopied sugar maple and beech. Relative species representation in association with sugar maple and beech in this sample thus appears to be primarily a measure of relative shade tolerance. The values in Table V are based on combined samples

TABLE V. *Relative tolerance as indicated by the ratio of actual occurrence to random expectation in sugar maple and beech habitat range*

| Species | No. trees in sample | Ratio A/R | Rating |
|---|---|---|---|
| Sugar maple | 118 | 1.34 | Very tolerant |
| Beech | 664 | 1.33 | Very tolerant |
| Hickory | 106 | .91 | Intermediate |
| Red oak | 27 | .85 | Intermediate |
| Basswood | 16 | .65 | Intermediate |
| White oak | 63 | .62 | Intermediate |
| White ash | 62 | .62 | Intermediate |
| Elm | 28 | .32 | Intolerant |

of the associates of sugar maple and beech witness trees. The low ratio for elm indicates low tolerance. The high ratios for beech and maple indicate the high degree of tolerance which typifies these species (Burns 1923) and the relative values for other species are generally consistent with field observations and standard tolerance tables (Toumey and Korstian 1947, Baker 1949). The figures for hickory and elm are least consistent with the published tables. This can be explained in the first case by the high incidence of the relatively tolerant shagbark hickory (*Carya ovata*) and by the presence of some bitternut hickory (*Carya cordiformis*) which is also relatively tolerant. Chance variation in a small sample may account in part for the low figure for elm, but the pronounced increase in abundance of elm in the modified secondary forests where the canopy has been opened up (Root 1941) supports the "intolerant" rating of Table V for this region.

While the decreased representation of other species in the beech-maple range is too consistent to be denied, another factor may well contribute to the bimodal tendency of the white oak and hickory curves—the lumping of species with different modal points. There is a strong probability that swamp white oak (*Quercus bicolor*), bur oak (*Q. macrocarpa*), and chinquapin or yellow oak (*Q. muehlenbergii*) were thus lumped with white oak in some of the surveys. While numerically unimportant, they would contribute slightly to the secondary peak in the moist habitat range. Similarly, bitternut hickory (*Carya cordiformis*) may be in part responsible for the bimodal character of the hickory curve, for its mode apparently lies to the right of that of shagbark hickory (*Carya ovata*), the more abundant species.

## SUMMARY AND CONCLUSION

Witness trees in the land survey records for Shelby County, a typical sample area in the beech-maple region of western Ohio, provide a useful sample of composition and species association in the original forest cover. They are used to demonstrate:

(1) the regional predominance of beech, which made up 42% of the entire sample, more than four times the abundance of its nearest competitor;

(2) the existence of a widespread beech forest type which graded into beech-sugar maple only on the rolling to broken topography along the Great Miami River and its major tributaries;

(3) the shifts in forest composition from one major soil area to another due to soil moisture and aeration changes and competitive interrelationships of species;

(4) the existence of a forest *continuum* in which all major species are associated, but in which they differ in their degree of association in random pairs; and

(5) the extreme modification of the forest remnants of the area after a century of occupancy by white man.

The use of species as habitat indicators makes possible further analyses of the random pair data, which provide:

(1) species distribution patterns approximating a normal curve along a moisture gradient;

(2) a measure of contiguous distribution based on concentration of species in their self-defined habitat ranges;

(3) evidence of beech and sugar maple dominance in the consistent underrepresentation of other species in association with them; and

(4) a measure of shade tolerance based on degree of representation of species in the mesic beech-sugar maple habitat range, which, except for the presence of beech and sugar maple, would be a favorable habitat for all the major species in the sample.

It is concluded that random pairs of trees constitute an especially useful tool for the analysis of organizational pattern in the forests of a region. They provide an efficient basis for composition inferences and at the same time yield information on habitat ranges of participating species and competitive interrelationships among species.

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# A PRELIMINARY ANALYSIS OF THE PHYSICAL ENVIRONMENT OF THE NORWAY RAT[1]

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It is now generally recognized that the physical environment plays an important role in limiting populations of animals, but an understanding of the extent of this role depends largely upon the recognition and measurement of the major environmental factors involved. Much work has been done on the qualitative aspect of the problem, particularly descriptions of factors considered important, but such items as food and space have all too long escaped the yardstick. The object of this paper is to present the results of a series of observations and experiments attempting to quantify the physical environment of a feral population of Norway rats (*Rattus norvegicus*) in Baltimore, Maryland. A more detailed investigation into the evaluation of domestic garbage as food for rats is being published separately (Schein and Orgain 1953).

Information relating to the rat's environment was obtained by environmental surveys of experimental residential areas, in cooperation with the Rodent Control Division of the Baltimore City Health Department. The "experimental areas" have been under observation since 1944 and records of rat populations have been kept by the Division of Vertebrate Ecology of the Johns Hopkins University School of Hygiene and Public Health. This information made it possible to select blocks in which the rat population was relatively stationary.

In order to measure the environmental factors in terms of numbers of rats, it was necessary to select only those blocks with rat populations close to the carrying capacity of the block. Hence, if a factor could be determined to be the limiting one for a particular population, a measurable reduction in this factor should result in a reduction in the rat population, which is also measurable. In this way it should be possible to determine the unit of factor corresponding to a unit of rat population.

The unit of area selected for survey purposes was a city block bounded on all 4 sides by paved city streets, which Davis *et al.* (1948) report form fairly effective natural barriers to random rat movements. The Baltimore city block is characterized by 2- or 3-story brick structures arranged in solid rows facing the streets, and having narrow back yards which extend to an alleyway which usually runs the length of the block. Solid wooden fences constructed along the property lines generally separate the yards in the rear. Portions of many yards are paved with concrete or brick, which, when defective or improperly constructed, form excellent harborage for rats.

A survey form had been developed by A. H. Holloway (unpublished ms.) that contained all the principal environmental factors. These factors were further divided into sub-classifications to fit the environmental conditions encountered throughout the survey area. This form was later revised by Charles Snyder (unpublished ms.), who introduced weighted values for the various factors. The form has been further consolidated by the senior author, and the weighted values were altered to fit the particular environment under study. In addition, minor

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environmental factors were omitted or classified under one of the existing categories. Likewise, the sub-classifications were reduced to 3 in number in order to have clear-cut limits and to avoid overlapping of condition definitions. The final listing of environmental factor categories and sub-classification descriptions is shown in Table I.

TABLE I. *Rodent Survey Environmental Factors and Subclassification Definitions*

A. Main Structure
1. Building completely ratproof
2. Building with rat entrances possible only through poorly fitting doors, windows, or screenings
3. Buildings with holes in foundation or walls

B. Appurtenance to Main Structure
1. Porch or room raised 2′ above ground, clean beneath
2. Porch or room raised 2′ above ground and with litter beneath; or raised less than 2′ but more than ½′ above ground
3. Porch or room raised less than ½′ above ground, or not raised at all

C. Sanitary Conditions of Back Yard (Harborage)
1. Clean
2. Some litter or orderly stored materials
3. Yard containing trash or junk heaps

D. Paved Area in Back Yard
1. Good paving adjoining foundation of building, without break
2. No paving adjacent to main structure
3. Broken paving or poor brickwork near foundation of building

E. Food Supply
1. Refuse in tightly closed metal container, or refuse not stored in yard at all
2. Refuse in open metal containers
3. Refuse in non-ratproof containers or not in containers at all

F. Fences
1. Yards with no fences, or with wire fences offering little or no harborage
2. Yards with solid fences offering harborage on less than ½ perimeter of yard
3. Yards with solid fences offering harborage on more than ½ perimeter of yard

G. Fowl or Animal Cages
1. Cages elevated 2′ above ground and clean beneath; cages set directly on a concrete apron
2. Cages elevated 2′ above ground with litter beneath; cages less than 2′ above ground, but more than ½′, no concrete beneath
3. Cages less than ½′ above ground, no concrete beneath

H. Miscellaneous Structures
1. Structure elevated 2′ or more above ground, clean beneath
2. Structure less than 2′ above ground, or on ground with unbroken concrete
3. Structure on ground with wooden, broken concrete, brick, or no floor

The actual survey of a block consisted of evaluating each yard according to the condition of each environmental factor as described by the sub-classifications. In order to obtain a satisfactory survey, it was necessary to examine carefully each environmental factor to avoid overlooking conditions which were not being used by the rats at the time of the survey. No notations were made as to the presence of rats except in the remarks column.

To eliminate possible bias on the part of the investigators, the degree of rodent infestation was determined by persons who had no access to the environmental survey forms at the time. The technique used to estimate the rat population (Emlen *et al.* 1949) is able to detect population changes of greater than 10 per cent, which was precise enough for the purposes at hand.

The sub-classifications of each environmental factor were weighted in accordance with the percentage of times the particular condition appeared together with the degree of rat infestation in a yard. An example of the derivation of the weighted values expressed in terms of the above may be stated as follows:

$$W = \frac{(0S_0 + 1S_I + 2S_{II} + 3S_{III})}{S_0 + S_I + S_{II} + S_{III}}$$

where $W$ = weighted environmental factor and $S_0$, $S_I$, $S_{II}$, $S_{III}$ = the percentage of times the particular sub-classification occurred in a yard with a rat infestation rating of *O*, *I*, *II*, or *III* (determined after comparing the environmental survey with the population survey). For convenience, the final value was multiplied by 10. As an example, if an area

contained 100 structures listed by the authors under sub-classification 1 (completely ratproof), of which 54 had rat infestation ratings of *O*, 26 of *I*, 12 of *II*, and 8 of *III* (as determined by the population survey), then:

$$W = \frac{((0 \times 54) + (1 \times 26) + (2 \times 12) + (3 \times 8)) \times 10}{54 + 26 + 12 + 8} = 7.4$$

The weighted environmental values appearing in the three columns of Table II were calculated from over 60 block surveys and represent an average value corresponding only to the conditions existing within the experimental area at the time (1948-1950) the surveys were made.

TABLE II. *Weighted environmental values of subclassifications within the experimental area*

| | *Subclassification* | | |
|---|---|---|---|
| *Environmental factor* | 1 | 2 | 3 |
| Main structure | 7.4 | 8.2 | 9.5 |
| Sanitary conditions of backyard | 7.0 | 8.5 | 10.1 |
| Paved areas | 6.6 | 9.2 | 10.7 |
| Food supply | 7.2 | 8.7 | 9.8 |
| Fences | 5.6 | 9.4 | 8.7 |

## MINIMUM ENVIRONMENTAL FACTORS

Consider the relationship obtaining between a rat population and an environmental factor, such as the amount of water available to the population. When the factor is at zero, *i.e.*, no water whatsoever available, then the population of the area would also be at zero. Up to a certain point, for every unit increase in factor supply (in this case, water) there would be a unit increase in population. Above this point, a unit increase in factor results in a correspondingly smaller increase in population, until finally an increase in factor results in a negligible (if any) increase in population. What has happened is that the factor (water) governed the size of the population until some other factor, such as available space, became more important to the growing population. Above that point, the factor (water) is surplus and great fluctuations in amount are no longer important to the population, so long as the critical governing point, or minimum point, is not reached. It is recognized that even in the limiting phase of a factor, the relationship between it and the population is not always linear, but this is often due to the interplay between internal (physiological) factors and the external factor under consideration. (For a more detailed and comprehensive discussion of density-dependent factors, the reader should consult a standard text on animal ecology, such as Allee *et al.* (1949)).

For the purposes of this study, those environmental factors that showed a positive correlation with the population size were considered to be, at that time and place, *limiting* factors, *i.e.*, at or below the critical minimum with respect to the population size. When a positive correlation was not apparent, the factor involved was considered to be clearly in excess of the population needs.

The environmental values for a particular block in the experimental area were plotted with respect to the population size as shown in Figure 1. Examination of this figure reveals that food supply, paved areas, and main structures are positively correlated with population, while no positive correlation seems to

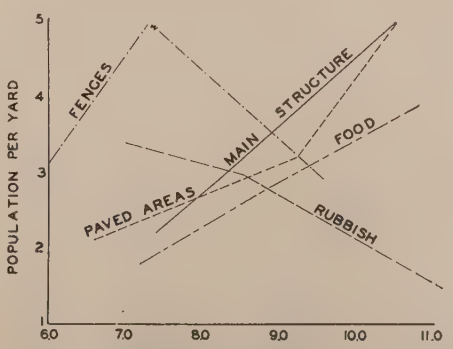


FIG. 1. Relation of population per yard to weighted environmental value of various factors.

exist between the population and the condition of fences or the amount of rubbish in the yards. Therefore, in this particular block, the fences and rubbish are clearly in excess of the population needs and are considered factors of potential, rather than actual, harborage. Theoretically, the quantity of harborage area could be reduced a great deal, without any serious long term effects on the population, before reaching the critical minimum.

To test this hypothesis, an experiment was conducted to see what would happen when an actual harborage factor is reduced in an environment which also contains a great deal of potential nesting area. Figure 2 represents the rat population,

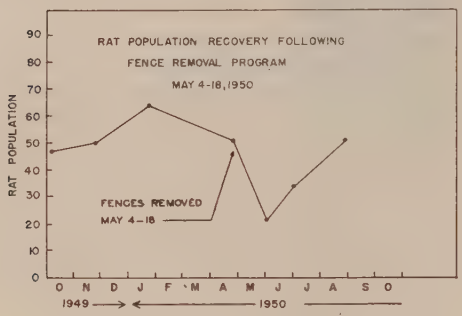


Fig. 2. Recovery of a rat population following the removal of an active harborage factor, potential harborage area remaining essentially undisturbed.

over a period of time, of a city block in which solid wooden fences served as the actual harborage sites for a large percentage of the rat population. The environmental survey indicated that defective pavement was slightly in excess of the population needs and that piles of lumber and junk were clearly in excess of the requirements; these were the potential areas of harborage.

During May, 1950, the Baltimore City Health Department enforced the usual sanitary regulations by requiring property owners to remove all wooden fences, including the bottom boards of wire fences wherever they made contact with the ground. In addition to the removal of the fences some occupants voluntarily repaired broken concrete areas and cleaned up trash piles. No attempt was made to control refuse at this time, but it was evident that some reduction in the amount of scattered refuse occurred when the back yards were exposed. As a result of these activities, the rat population fell to about half its previous value, according to a survey conducted one month afterward. However, the next survey, conducted in July, indicated a rising population, and by September, 1950, the population was about as high as it originally had been when the fences were first removed. This is interpreted as meaning that the survivors of the May cleanup became established in new nesting locations heretofore considered as "potential" harborage areas, and rapidly set about to realize the unaltered carrying capacity of the block. Apparently, then, something other than harborage area was setting the upper limit of the carrying capacity of the area. These studies indicated that *food* was probably the limiting, or minimum, factor in many of the experimental blocks, and the investigation was redirected accordingly.

### Garbage Control and Its Effect

In February, 1950, an entire city block was selected to test the effect of refuse control as a means of reducing the existing rat population. The rat population in this block had been measured at bimonthly intervals since March, 1949, and indications were that the population was essentially stationary and at carrying capacity at the start of the refuse reduction test (Fig. 3).

With the aid of city authorities, property owners were asked to use rat-proof containers of sufficient capacity to contain all the refuse produced on the premises between periods of regular collections. This was effective in most instances and undoubtedly improved the overall refuse storage, but at no time were all the premises supplied with adequate

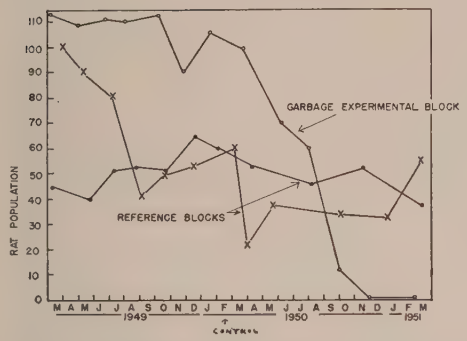


FIG. 3. Populations in the experimental and two control blocks, showing the decline in the experimental block following refuse control procedures.

containers, nor were all the existing containers equipped with tight-fitting lids. Numerous inspections of the area revealed that approximately one-third of the premises were deficient in some way, a greater proportion of these deficiencies being uncovered refuse containers. Relatively few housholders were habitual violators, but almost all were deficient on at least one occasion. Three city blocks were originally proposed for these studies, but the enforcement of sanitary regulations proved to be such a task that all effort of control was confined to one block and the other two were kept undisturbed as reference blocks.

In February, 1950, an environmental survey made by the senior author indicated that food was clearly in excess of population needs. A 50 per cent reduction of the food supply (author's estimate) was accomplished by inspections but had no clearcut effect on the population size. However, indications were that by May, 1950, food had been reduced to the critical minimum point described above, and at this time the sanitary regulations were again enforced resulting in an additional 25 per cent reduction of the food supply. The number of dead rats found in the alleyway and in the yards increased noticeably (verbal reports of the inhabitants); on some occasions as many as 5 or 6 dead rats were counted by the authors in one colony area. Many of the smaller colonies disappeared in a relatively short time and there was evidence of decreased activity in the larger colonies. By September, 1950, only 2 colonies persisted in the block, one of which was located across the alley from the refuse storage space used by a restaurant, and the other under a concrete slab upon which the refuse cans and accumulations from an apartment house were stored. Both sites normally contained refuse stored in open cans or in nonratproof containers. However, without any additional effort by the authors or the city authorities to control the refuse situation, the rat population in the block dropped to zero within the next few months. The population decline in the experimental block, as compared to the relatively stationary populations of the reference blocks, is shown in Figure 3.

### Experimental Feeding of Rats

The purpose of these feeding experiments was to determine some of the characteristics of food as an environmental factor. A well isolated colony of rats, covering a total area of approximately ¼ city block, was provided with feeding stations. To force the rats to eat from the controlled stations, it was necessary to have absolute control of the garbage situation within the normal range of rat activity. Since studies by Davis *et al.* (1948) on the home range of the Norway rat indicate that rats seldom travel more than 100-150 feet, householders whose yards were within a radius of 200 feet of the periphery of the colony were requested to place all food wastes in small garbage cans which were furnished by the investigators. The garbage containers were kept on the back steps and daily collections were made by the authors; this latter procedure was received with enthusiasm by the householders and thereby insured full cooperation during the course of the experiment.

Feeding stations were established in 3

of the yards which lay within the estimated range of the rats. The stations were plywood boxes, about 2 x 3 x 2 feet, with a hinged top and 3-inch holes opened near the base to provide the rats ready access to the interior. Food (garbage) was placed within the stations in trays, which permitted easy removal for weighing, and the boxes were kept locked to minimize disturbance from larger animals and children.

After a short period of time the rats accepted the garbage offered in the boxes and the colony was fed in this manner during a period of about 3 months. The consumption of garbage increased steadily and it was soon evident from reports of the local inhabitants that there was a noticeable increase of rat activity within the area; this activity is presumed to indicate an increase in the rat population. Repressive measures taken by the residents of the area were sporadic, and apparently failed to hamper the colony growth; few of the residents noted the connection between the feeding stations and the increased colony activity.

The colony was trapped for a period of about 5 days during mid-August, 2½ months after the stations were set up; 16 rats, totalling 3870 gm. were removed, and consumption from the stations dropped to about ½ of the peak level. However, at the end of trapping operations the average daily consumption increased to its original level within 2 weeks. Since 2 weeks is not sufficient time for reproduction to replace the 3870 gm. of rats removed, and since the colony itself was well enough isolated to preclude immigration from the outside, it appears that not all the rats in the original colony had had full access to the feeders. Figure 4 shows the rate of increase of consumption following periods of trapping, and suggests that the colony had actually grown to a point where only a portion of the rats had full access to the food supply at any time. The secondary rats probably fed to a great extent on morsels

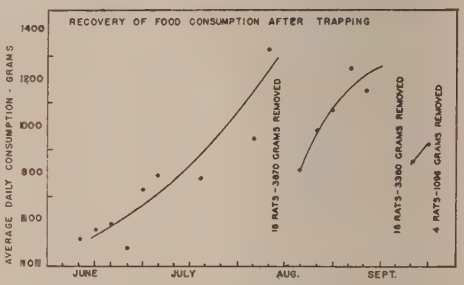


FIG. 4. Changes in food consumption of isolated rat colony following periods of trapping.

of food that were dragged out of the food boxes by the primary rats and left only partially consumed.

The colony was later intensively trapped and found to contain approximately 40 rats. The fact that, after the first trapping period when 40 per cent of the population was removed, the average daily consumption increased to its original level within a period of 2 weeks would indicate that the *distribution,* rather than the *quantity* of food was directly controlling the numbers of rats. Had the same amount of food been more widely distributed in the same area, it seems possible that the consumption would have been much more than the maximum shown.

By recording the type of foodstuffs remaining in the feeding trays each day, it was soon realized that rats generally refused most vegetable wastes and parings. Often the garbage collected from the residents was largely made up of non-preferred foods, and therefore great quantities of garbage were offered in the feeding stations so that at least a minimum of the more preferred types, such as bread and meat, would be included.

A more detailed analysis of foods preferred by the rats, as determined from a series of concurrently run experiments, is presented in a report by Schein and Orgain (1953).

## SUMMARY

This paper attempts to evaluate the physical environment of a population of

Norway Rats (*Rattus norvegicus*). A survey form lists 8 major structural factors which would be important in assessing the amount of harborage available to the rat. Each structural factor was further divided into 3 sub-classifications depending upon the amount of harborage offered to the rats. Rat populations were estimated independently of the environmental surveys and the two were later compared. A method of quantifying a factor (from the rats' viewpoint) was developed and used to determine what environmental factors were correlated with the rat population. In any particular block, some factor was usually distinguishable as the limiting factor.

To test this hypothesis, the wooden fences which were considered to be in excess of population needs were removed with the cooperation of city authorities. The rat population dropped to about half its original value within one month, but was back to its original level 3 months afterward. These studies indicated that some other factor, probably *food,* was determining the upper limit of the carrying capacity of the area in most cases.

An investigation was initiated to determine the effect on the rat population of a sharp reduction in the amount of garbage available to them. Although the refuse of the block was never completely unavailable to the rats, the population was completely eliminated within 6 months. On the other hand, the populations of the 2 reference blocks were reasonably stationary.

A further study was designed to determine some of the characteristics of food as an environmental factor. Three feeding stations were set up, and the amount of food taken by the rats was measured daily. After about 3 months of feeding, 40 per cent of the colony was removed by trapping, but the total consumption intake from the feeding stations was reduced for a period of only 2 weeks, after which consumption progressed at essentially the same high level. This would indicate that not all the rats in the colony had direct access to the feeding stations, and therefore the *distribution* as well as the *quantity* of food should be taken into consideration when studying the food factor.

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# THE STATISTICAL EFFICIENCY OF SAMPLE PLOT SIZE AND SHAPE IN FOREST ECOLOGY

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## Introduction

"The need for quantitative records [of vegetation] has made it necessary to give serious consideration to methods of sampling. Usually the members of an entire community cannot be counted or measured, and even if this were done, the information would be no more useful or significant than an adequate set of data acquired by proper sampling. Since this is true, it becomes of prime importance to determine what constitutes an adequate sample in terms of the community as a whole and how to obtain such a sample with a minimum of effort" (Oosting 1948).

The recognition of this need for adequate sampling has led to much discussion of sampling techniques in the literature of ecology. But in spite of this, actual attempts to determine what constitutes an adequate sample have been limited to a few techniques. This determination in forest ecology has been based largely on the species-area curve (Cain 1938) or on wholly empirical methods.

The importance of information obtained by either of these methods cannot be evaluated statistically. The former because, according to Ashby (1936), the requisite procedure for verifying the species-area equations is to take the readings of the number of species in plots of different sizes laid at random over the community. It is not legitimate to compose the readings for larger plots by combining the data from smaller ones, for this treatment cancels out any inequalities in distributions. Since most of the data purporting to verify these equations have been collected in this statistically erroneous way, it is impossible at this time, to evaluate the equations statistically. Empirical methods, including the systematic sample, cannot be evaluated or interpreted statistically because the random sample is the only safe basis for statistical calculation.

Some application of statistical method (in the sense of the statistician) has been made to the problems of ecological sampling (Clapham 1932, Ashby 1935 and 1936, Pechanec and Stewart 1940, Penfound 1945, and others). Although most applications have dealt with non-forest vegetation, foresters of the U. S. Forest Service have employed statistical methods to determine the size and number of plots necessary for the purposes of timber cruising and for estimating forest tree reproduction.

### *The statistical technique*

The objective of this project has been to use a modification of Clapham's method to determine the most effective size and shape of plot for sampling trees > 1 inch d.b.h. in a climax oak-hickory forest. Clapham (1932) used statistical variance to make this determination on herbaceous vegetation.

Variance, when used in this way, is a measure of dispersion among observations (Schumacher and Chapman 1947) and, as such, it can be used to determine the most effective type of sampling unit. This use is explained by the following example.

[1] This work was done at Duke University and with use of facilities of the Department of Botany. Thanks are due to Professors H. J. Oosting and F. X. Schumacher for advice, respectively, on the ecological phases and statistical aspects of this study.

A square area is divided into 16 equal smaller units or plots. A population of 48 objects is scattered among these 16 plots in the following manner:

| | A | B | C | D |
|---|---|---|---|---|
| A′ | 3 | 0 | 5 | 1 |
| B′ | 5 | 7 | 2 | 0 |
| C′ | 3 | 2 | 0 | 7 |
| D′ | 3 | 3 | 3 | 4 |

The average number of objects per plot would be *3*. The deviation from the average of the observation (number of objects) on each plot would be that observation minus *3*. Thus, the deviation of observations *A′A, A′B, A′C,* and *A′D* could be, *0, —3, 2, —2* respectively. Squaring the deviations eliminates negative numbers, and, in addition the final data can be submitted to further statistical manipulation (Snedecor 1946). The sum of the individual squared deviations divided by the number of observations from which the deviations were obtained represents the variance of each observation obtained on this particular size of plot.

This can be represented symbolically as

$$\frac{1}{n} S^n[(y - \bar{y})^2] = V(y)$$

where $y$ represents the individual observed value on each plot; $\bar{y}$ represents the average value per plot; $S^n$ $[(y - \bar{y})^2]$ represents the summation of all the individual deviations from the average squared; $n$ represents the number of observations; and $V(y)$ represents the variance of each observation.

If each plot in the example contained 3 objects, or an observation of 3, the $V(y)$ would be zero. If one plot contained 48 objects and the 15 remaining plots contained none, the $V(y)$ would be 135. Thus, variance is a measure of consistency or dispersion among observations, ranging from zero, when the observations are identical, through small values when they are fairly consistent, to high values as they become discordant (Schumacher and Chapman 1948).

The population of the example could be regrouped in many ways by regrouping the small plots into larger ones, as shown in Table I.

TABLE I. *The possibilities for regrouping 16 1×1 plots into plots of different size and shape*

| Plot size | Direction of longest axis | Number of plots | No. of 1x1 Plots contained in one larger plot | Shape of plot |
|---|---|---|---|---|
| 1 x 1..... | ..... | 16 | .. | Square |
| 1 x 2..... | (Horizontal) | 8 | 2 | Rectangle |
| 2 x 1..... | (Vertical) | 8 | 2 | Rectangle |
| 2 x 2..... | ..... | 4 | 4 | Square |
| 1 x 4..... | (Horizontal) | 4 | 4 | Rectangle |
| 4 x 1..... | (Vertical) | 4 | 4 | Rectangle |
| 2 x 4..... | (Horizontal) | 2 | 8 | Rectangle |
| 4 x 2..... | (Vertical) | 2 | 8 | Rectangle |

After regrouping, the variance of the observations on each of the new plot shapes can be obtained by using the method already described. These variances, obtained from observations on plots of different area, must be reduced to the basis of unit area, or in this case to the basis of the smallest plot, before they can be directly compared.

Inspection of the variances, following the reduction, would reveal the plot shape with the smallest variance. This plot shape would sample the population with the greatest consistency, and, consequently, it would be the most efficient plot shape of those tested.

This point can be illustrated by regrouping the 1 × 1 unit plots of the example, computing the variances, reducing them to the 1 × 1 unit basis, and comparing the final variances to determine the most efficient size plot.

1 x 1

| | | | |
|---|---|---|---|
| 3 | 0 | 5 | 1 |
| 5 | 7 | 2 | 0 |
| 3 | 2 | 0 | 7 |
| 3 | 3 | 3 | 4 |

$$\frac{1}{n} S^n \left[ (y-\bar{y})^2 \right] = \frac{1}{16} S^{16} \left[ (y-3)^2 \right] = 4.625 = V(y)_1$$

1 x 2

| | |
|---|---|
| 3 | 6 |
| 12 | 2 |
| 5 | 7 |
| 6 | 7 |

$$\frac{1}{n} S^n \left[ (y-\bar{y})^2 \right] = \frac{1}{8} S^8 \left[ (y-6)^2 \right] = 8.000 = V(y)_2$$

To compare the final variances, they must all be put on the same unit basis. This is done by dividing the variances of the larger plots by the number of smallest (1 × 1) plots contained in the larger plot (*e.g.*, the variance of the 1 × 2 plot would be divided by 2 since it contained two 1 ×1 plots).

Therefore:

$$\frac{V(y)_2}{2} = \frac{8}{2} = 4.000$$

2 x 1

| | | | |
|---|---|---|---|
| 8 | 7 | 5 | 1 |
| 6 | 5 | 3 | 11 |

$$\frac{1}{n} S^n \left[ (y-\bar{y})^2 \right] = \frac{1}{8} S^8 \left[ (y-6)^2 \right] =$$

$$\frac{66}{8} = 8.250 = V(y)$$

reducing to *1 x 1* basis

$$\frac{V(y)_3}{2} = \frac{8.250}{2} = 4.125$$

1 x 4

| |
|---|
| 9 |
| 14 |
| 12 |
| 13 |

$$\frac{1}{n} S^n \left[ (y-\bar{y})^2 \right] = \frac{1}{4} S^4 \left[ (y-12)^2 \right] =$$

$$\frac{14}{4} = 3.500 = V(y)_4$$

reducing to *1 x 1* basis

$$\frac{V(y)_4}{4} = \frac{3.500}{4} = 0.875$$

4 x 1

$$\frac{1}{n}S^n\left[(y-\bar{y})^2\right] = \frac{1}{4}S^4\left[(y-12)^2\right] =$$

$$\frac{8}{4} = 2.000 = V(y)_5$$

reducing to *1 x 1* basis

$$\frac{V(y)_5}{4} = \frac{2.000}{4} = 0.500$$

2 x 4

$$\frac{1}{n}S^n\left[(y-\bar{y})^2\right] = \frac{1}{2}S^2\left[(y-24)^2\right] =$$

$$\frac{2.000}{2} = 1.000 = V(y)_6$$

reducing to *1 x 1* basis

$$\frac{V(y)_6}{8} = \frac{1.000}{8} = 0.125$$

4 x 2

$$\frac{1}{n}S^n\left[(y-\bar{y})^2\right] = \frac{1}{2}S^2\left[(y-24)^2\right] =$$

$$\frac{8.000}{2} = 4.000 = V(y)_7$$

reducing to *1 x 1* basis

$$\frac{V(y)_7}{8} = \frac{4.000}{8} = 0.500$$

2 x 2

$$\frac{1}{n}S^n\left[(y-\bar{y})^2\right] = \frac{1}{4}S^4\left[(y-12)^2\right]$$

$$\frac{30}{4} = 7.500 = V(y)_8$$

reducing to *1 x 1* basis

$$\frac{V(y)_8}{4} = \frac{7.500}{4} = 1.875$$

When the resulting variances are tabulated, it is apparent that certain plot shapes show much less variation than others.

| | | Second given dimension of plot size | | |
|---|---|---|---|---|
| | | 1 | 2 | 4 |
| First given dimension of plot size | 1 | 4.625 | 4.000 | 0.875 |
| | 2 | 4.125 | 1.875 | 0.125 |
| | 4 | 0.500 | 0.500 | |

These plots, with the smallest variance, would produce the most consistent samples when employed in sampling this population.

It should be added that these variances in themselves are misleading in that such a very limited population does not lend itself to this type of statistical treatment. Also, many workers who have employed this method with large biological populations have found that the smallest size plot usually has the smallest variance and

that with an increase in size of the plot there is an increase in variance (Hasel 1938, Yates and Zacopanay 1935, and others).

The method described in this example was used to determine what size and shape of plot would be preferable for use in sampling an oak-hickory (*Quercus-Carya*) forest.

*The forest and site of the study*

The original idea, on the selection of the study site, had been to find an area with a homogeneous forest located on terrain sloping in one direction. Unfortunately, the Piedmont in the region of Durham, North Carolina, the location of the study, is highly disturbed and well-developed oak-hickory forests of large extent are relatively scarce. Consequently, the final selection of a site represented a compromise.

A 140 × 140m area in the Duke Forest was selected. One corner of this area was near the crest of a small hill, and although slopes fell away in two directions, one slope was much more pronounced than the other (Fig. 1).

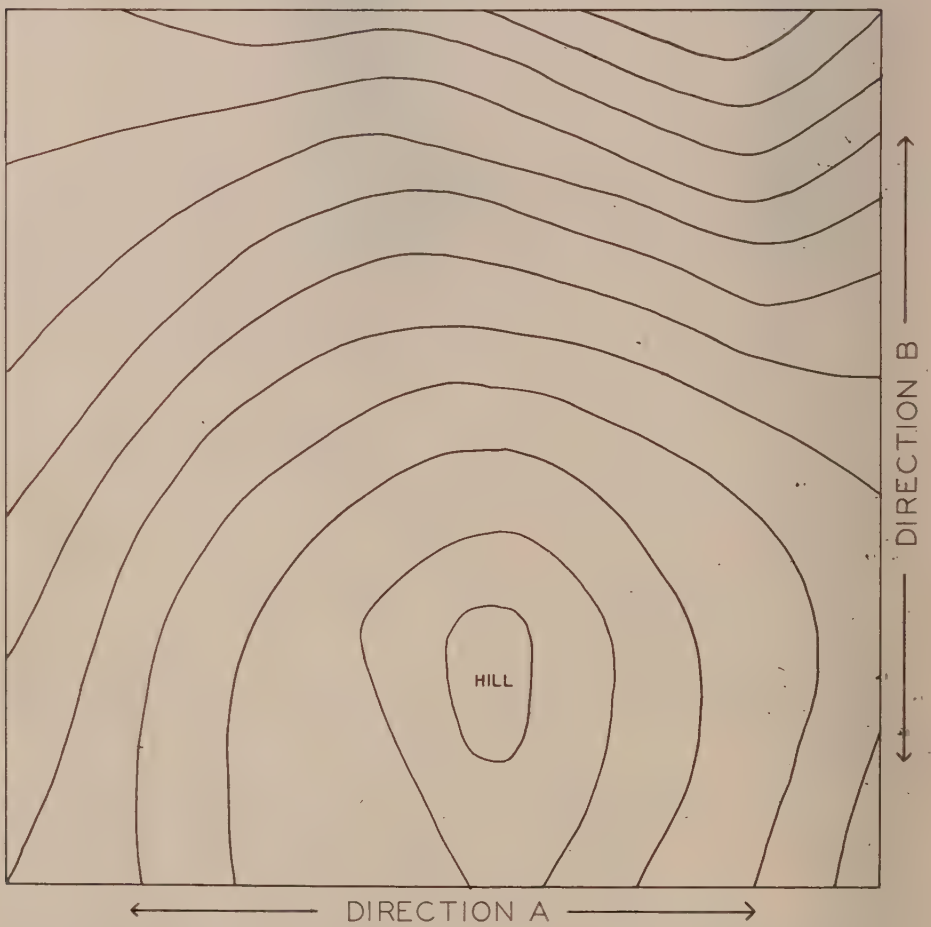


FIG. 1. Contour map of the experimental area. The small elliptical area represents the crest of a hill.

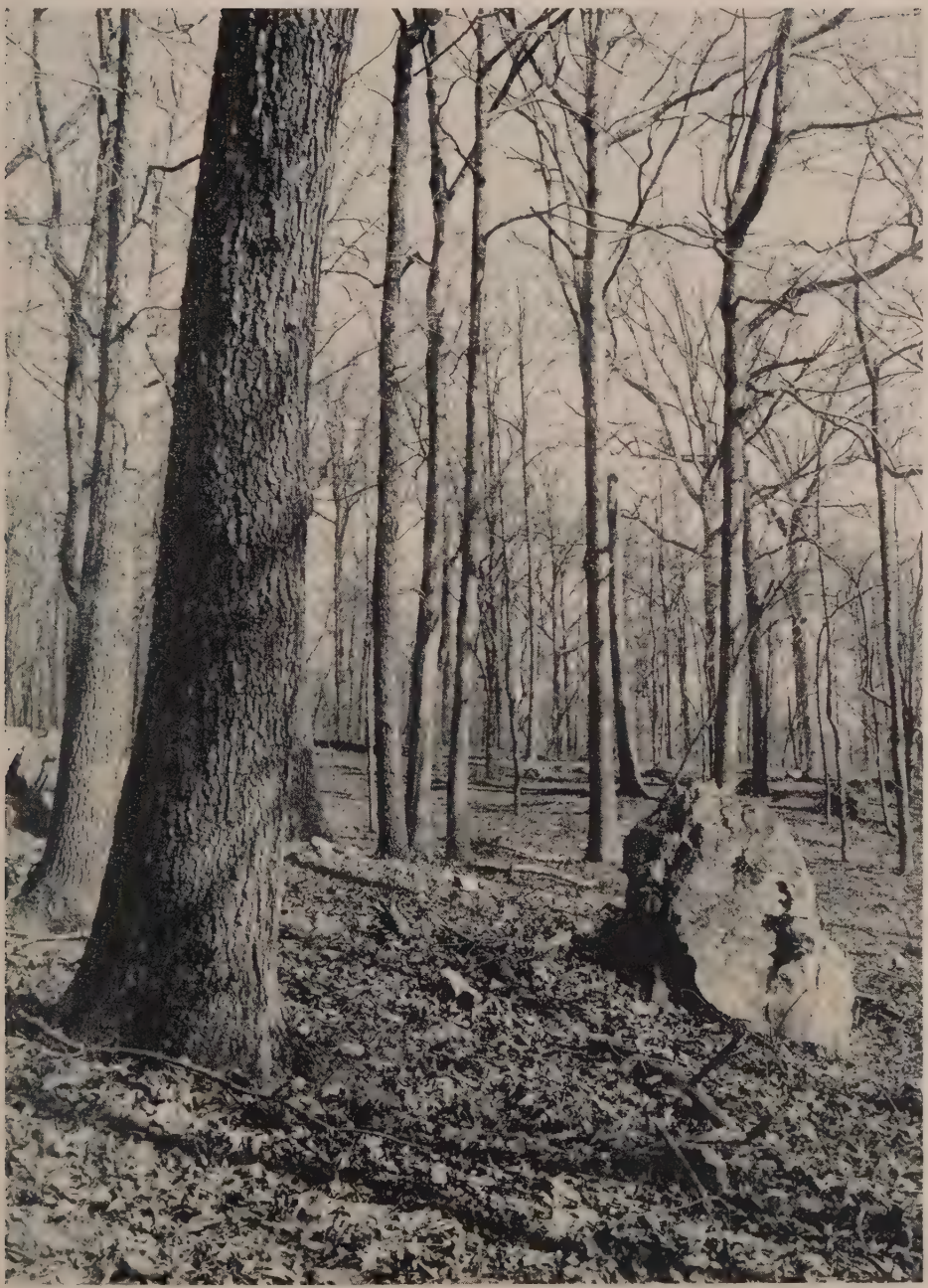

FIG. 2. Experimental area in winter aspect. Photograph by Charles Farrell.

Three soils, all derived from the Carolina Slate Formation, covered the area. The crest of the hill was one type, while the other two types occurred as broad bands below the crest. In general, the whole area was very rocky and, un-

doubtedly, was of low site quality. Perhaps this is one of the reasons why it was relatively undisturbed.

The forest covering the area would be classified as an upland white oak-red oak-black oak-hickory forest (Oosting 1942). On the whole, it appeared to be relatively undisturbed (Fig. 2). The absence of stumps and fire scars indicated that there had been no recent cutting or burning. However, one sign of disturbance was the presence of many twin sprouts. Increment borings of these twins revealed that most of them were between sixty and seventy years of age. Possibly they were the result of some past cutting or grazing.

The stand itself was uneven-aged with trees 120 years old or older uniformly scattered throughout to indicate that the site must have been covered with oak-hickory forest for at least that length of time. The stand, therefore, represented a relatively undisturbed, immature climax forest.

## Method and Results

The area, 140 meters square, was divided into 4900 2 × 2m plots, the smallest units used. All of the trees one inch d.b.h. or more were mapped in accordance with their occurrence in the plots. Thus, the exact location of all the trees within the area was obtained.

The basal area of these trees was used as the observational unit. The reason for its use was that it represented a quantitative expression of dominance that could be easily measured in the field.

Rather than use the basal area of all trees in the calculation of variance, two groups or distributions were used. Distribution 1, containing 82.5% of the total basal area, was chosen to represent a "type" vegetation or that vegetation which is widely and evenly distributed over the area. Distribution 2, containing only 10.8% of the total basal area, was chosen to represent a smaller group more or less sporadically distributed over the area (Table II).

Table II. *Percentages of total basal area of each distribution occurring in each quarter of the area*

| Distribution 1 | | Distribution 2 | |
|---|---|---|---|
| 26.2% | 23.7% | 20.7% | 35.3% |
| 24.9% | 25.4% | 29.3% | 14.6% |
| Difference between high and low 2.5% | | Difference between high and low 20.7% | |

The object in using two distributions was to determine whether the plot most efficient in sampling the "type" vegetation would also be efficient in sampling lesser vegetation occurring on the same area.

Thus, for each of the 4900 plots there were two observations: the total basal area of all species in Distribution 1 occurring on each plot; and the total basal area of all species in Distribution 2 occurring on each plot.

The variances for each distribution were calculated separately. In other words, the variance of the observations in Distribution 1 was calculated for the 2 × 2m plot size. The 2 × 2m plots were then regrouped into 2 × 4m plots; the Distribution 1 observations on each of the 2 × 2m plots contained in each 2 × 4 were added to form the observation on the latter plot. The variance for these new observations was obtained and reduced to the 2 × 2m basis.[2]

[2] Because the form of the equation used in the calculation of variance in the introductory example becomes cumbersome when applied to large populations, the following variation was employed:

$$V = \frac{\frac{S(y^2)}{n_1} - \bar{y}S^n(y)}{\frac{n}{n_1}}$$

where $\bar{y}$ $S^n(y)$, the correction term for the smallest size plot, is used for all plots, where $n_1$ is the number of smallest size plots contained in the larger size plot whose variance is being calculated, and where $n$ is the total number of smallest size plots.

This process was repeated until the reduced variances for observations in Distribution 1 over all plot sizes had been obtained. Following this, the reduced variances for observations in Distribution 2 were obtained in the same manner.

Table III shows how the the 2 × 2m plots were regrouped. The variances obtained for the different plot groupings are represented in Figures 3 and 4. Figure 3 represents, for Distribution 1, the trend of the variance for plots of certain width as the length of the plot is increased. Figure 4 represents similar data for Distribution 2.

TABLE III. *Plot sizes and shapes resulting after regrouping 4900 2×2m plots in various ways*

| Size of plot in meters | Number of plots after regrouping | Direction of main axis (See Fig. 1) |
|---|---|---|
| 2 x 2 | 4900 | Square |
| 2 x 4 | 2450 | A |
| 2 x 4 | 2450 | B |
| 2 x 10 | 980 | A |
| 2 x 10 | 980 | B |
| 2 x 20 | 490 | A |
| 2 x 20 | 490 | B |
| 2 x 70 | 140 | A |
| 2 x 70 | 140 | B |
| 2 x 140 | 70 | A |
| 2 x 140 | 70 | B |
| 4 x 4 | 1250 | Square |
| 4 x 10 | 490 | A |
| 4 x 10 | 490 | B |
| 4 x 20 | 245 | A |
| 4 x 20 | 245 | B |
| 4 x 70 | 70 | A |
| 4 x 70 | 70 | B |
| 4 x 140 | 35 | A |
| 4 x 140 | 35 | B |
| 10 x 10 | 196 | Square |
| 10 x 20 | 98 | A |
| 10 x 20 | 98 | B |
| 10 x 70 | 28 | A |
| 10 x 70 | 28 | B |
| 10 x 140 | 14 | A |
| 10 x 140 | 14 | B |
| 20 x 20 | 49 | Square |

Schumacher and Chapman (1948) point out a method for determining the number of plots necessary to sample with a desired degree of efficiency. The variance of $y$, $[V(y)]$, when divided by the number of observations gives the variance of the mean $y$, $[V(\bar{y})]$ :

$$\frac{V(y)}{n} = V(\bar{y})$$

Since the variance of $y$ for each plot size is known, the $V(\bar{y})$ can be equated to certain desired precision and the number of plots necessary to obtain that precision can be obtained for each plot size: $\frac{V(y)}{V(\bar{y})} = n$ (In this instance, $n$ is not corrected for a finite population).

Thus, the number of plots necessary to obtain an estimate of the average basal area such that the chances would be 2 to 1 that it would be within ±10 per cent of the true mean could be obtained by equating $V(\bar{y})$ to $(\frac{1}{10}$ *mean basal area*$)^2$.

Using this method, the number of plots necessary to obtain this degree of precision was secured for each plot size in Distribution 1. The number of plots thus obtained were in numbers of 2 × 2m plots since all of the variances had been reduced to this basis. These were converted to the number of original size plots, the size of the plots before the variances were reduced. Table IV presents the data.

The precision with which the plot sizes most efficient for sampling Distribution 1 will sample Distribution 2 will be discussed later under the section headed Size and Number of Plots.

## DISCUSSION

### *Plot shape*

The question as to the most suitable plot shape for sampling biological populations has been widely investigated in the fields of agronomy and forestry.

Kalamkar (1932), working with field plot techniques for sampling potato harvests, concluded that long narrow plots were more effective in reducing the variability of yield among plots. He reasoned that this result was due to the fact that long narrow plots tended to reduce the effect of soil heterogeneity.

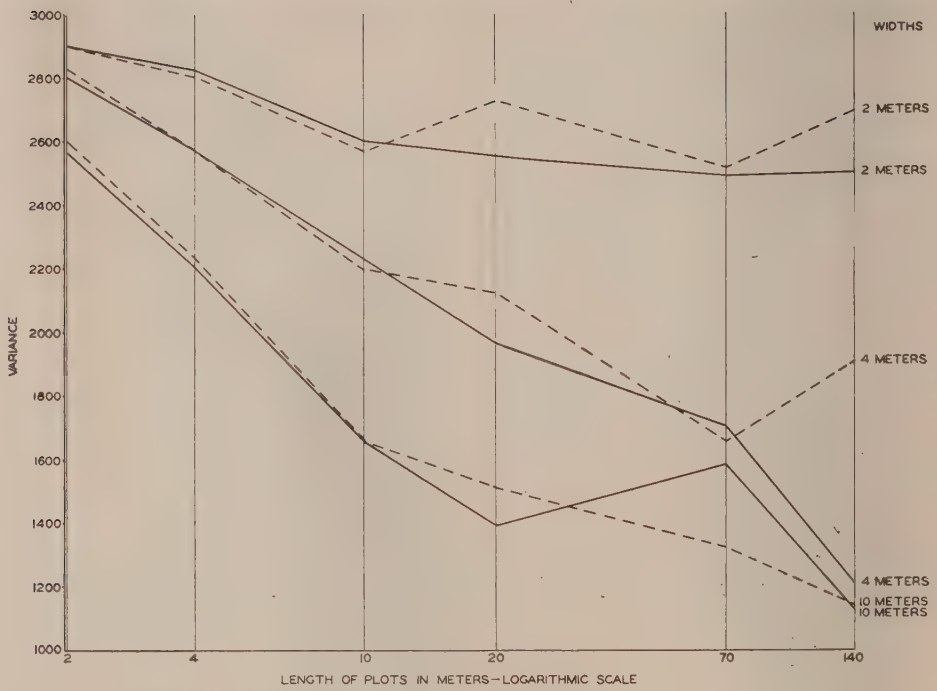


FIG. 3. Distribution 1. The change in variance of different width plots with an increase in the length of the plot (— — — plots running in Direction A, —— plots running in Direction B, see Figure 1 for directions).

Justesen (1932), also working with potato yields, came to the conclusion that long narrow plots were more efficient than shorter and wider ones of the same area. The same type of results were obtained by Clapham (1932) and Pechanec and Stewart (1940) who worked with natural populations. Hasel (1938) also found that in timber surveys the rectangular plot was superior to the square.

In most respects, the results of this investigation agree with the results of the aforementioned workers. It was found that variance per unit-area decreases as the sample plots are increased in length (Figs. 3 and 4, Direction B). However, this apparently applies only when the main axis of the plot runs against any observed contour or soil banding that occurs within the community under study. For Distribution 2, long narrow plots running with the contour were found to be distinctly less efficient than shorter plots of the same width (Fig. 4, Direction A).

It might be noted that Clapham (1932) found in his investigation on herbaceous vegetation that the longest narrowest plot was the most efficient. This was not the case here. The 10 × 140m plot in Distribution 1 and the 4 × 140m plot in Distribution 2 were both superior to plots of lesser width (see Figs. 3 and 4, Direction B).

Consideration should be given to the fact that although the long narrow plots give superior results, their use would entail more careful work. For the longer and narrower a plot is, the greater is its periphery in comparison to a square plot of the same area. Thus, the greater would be the possibility for making cumulative edge errors.

TABLE IV. *The area necessary to be sampled so that the chances will be 2:1 that the average basal area of the sample will be within ± 10% of the true average (Distribution 1)*

| Plot size (meters) | Direction of longest axis | Variance | Area in number of 2 x 2m plots | Number of 2 x 2m plots contained in larger plot | Area in number of larger plots | Percent of total area contained in sample |
|---|---|---|---|---|---|---|
| 2 x 2 | Square | 2898 | 1386 | 1 | ..... | 28.3 |
| 2 x 4 | B | 2830 | 1353 | 2 | 676.5 | 27.6 |
| 2 x 10 | B | 2599 | 1243 | 5 | 248.6 | 25.4 |
| 2 x 20 | B | 2555 | 1222 | 10 | 122.2 | 24.9 |
| 2 x 70 | B | 2490 | 1191 | 35 | 34.0 | 24.3 |
| 2 x 140 | B | 2503 | 1197 | 70 | 17.1 | 24.4 |
| 4 x 2 | A | 2803 | 1340 | 2 | 670.0 | 27.3 |
| 4 x 4 | Square | 2570 | 1229 | 4 | 307.3 | 25.1 |
| 4 x 10 | B | 2233 | 1068 | 10 | 106.8 | 21.8 |
| 4 x 20 | B | 1987 | 950 | 20 | 47.5 | 19.4 |
| 4 x 70 | B | 1704 | 815 | 70 | 11.6 | 16.6 |
| 4 x 140 | B | 1210 | 579 | 140 | 4.1 | 11.8 |
| 10 x 2 | A | 2567 | 1228 | 5 | 245.6 | 25.1 |
| 10 x 4 | A | 2198 | 1051 | 10 | 105.1 | 21.4 |
| 10 x 10 | Square | 1658 | 793 | 25 | 31.7 | 16.2 |
| 10 x 20 | B | 1392 | 666 | 50 | 13.3 | 13.6 |
| 10 x 70 | B | 1586 | 758 | 175 | 4.3 | 15.5 |
| 10 x 140 | B | 1128 | 539 | 350 | 1.5 | 11.0 |
| 20 x 2 | A | 2728 | 1305 | 10 | 130.5 | 26.6 |
| 20 x 4 | A | 2126 | 1017 | 20 | 50.9 | 20.8 |
| 20 x 10 | A | 1510 | 722 | 50 | 14.4 | 14.7 |
| 70 x 2 | A | 2515 | 1203 | 35 | 34.4 | 24.6 |
| 70 x 4 | A | 1650 | 789 | 70 | 11.3 | 16.1 |
| 70 x 10 | A | 1323 | 633 | 175 | 3.6 | 12.9 |
| 140 x 2 | A | 2696 | 1289 | 70 | 18.4 | 26.3 |
| 140 x 4 | A | 1901 | 909 | 140 | 6.5 | 18.6 |
| 140 x 10 | A | 1136 | 543 | 350 | 1.6 | 11.1 |
| 20 x 20 | Square | 1286 | 615 | 100 | 6.2 | 12.6 |

*The direction of sampling*

The way in which the rectangular plot is placed on the surface of the area is of importance. For example, foresters have long recognized the existence of banding in woodland populations, with better sites along the lower slopes and poorer sites commonly along the ridges. They have found that the efficiency of sampling such populations is enhanced if the sample plots cut across these bands (Schumacher and Chapman 1948, Hasel 1938).

This study indicates that the same situation holds here. A comparison of the variances of plots running in Direction B with those running in Direction A (Figs. 3 and 4) indicates that those plots whose longest axis is predominantly against the contour lines (Direction B, see Fig. 1) show the least variance.

A further indication of this may be had by the addition of the variances for all plots with their longest axis in Direction A and all plots with their longest axis in Direction B. This indicates that for Distribution 1 those plots with their longest axis in Direction B are 4 per cent less variable than those in Direction A. The same comparison for Distribution 2 shows that plots running in Direction B are 58 per cent less variable than those running in Direction A.

From this it would appear that when rectangular plots are employed they should be arranged so that the longest axis crosses the contour lines, or crosses any observed vegetational or soil banding within the community. It would seem that this would be of particular importance when the sampler is concerned with the lesser species occurring sporadically

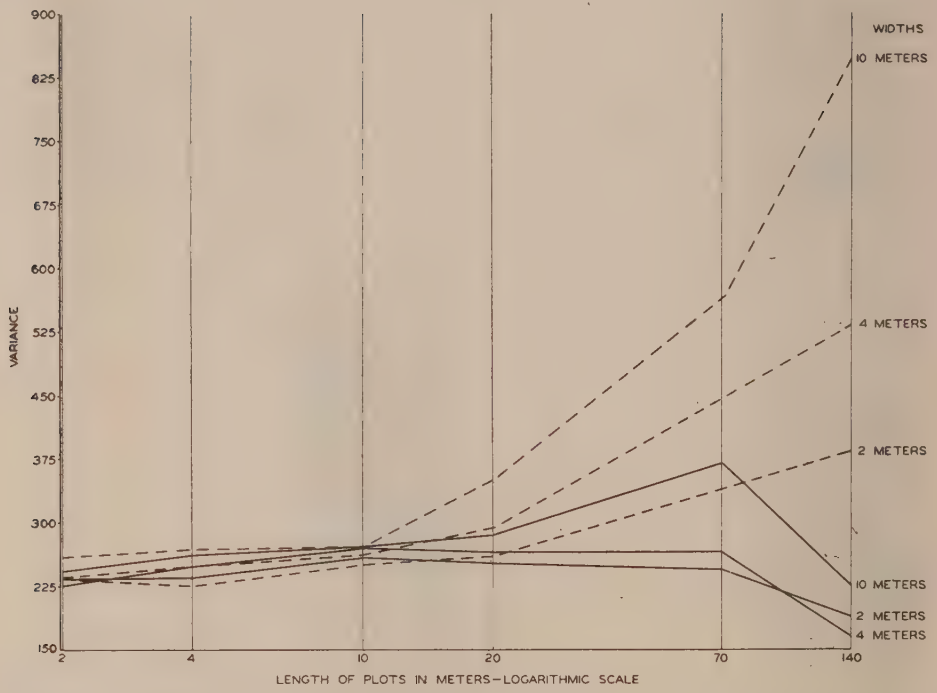


FIG. 4. Distribution 2. The change in variance for different width plots with an increase in the length of the plot (— — — plots running in Direction A, —— plots running in Direction B, see Figure 1 for directions).

throughout the dominant forest vegetation.

### *Size and number of plots*

Inspection of Table IV indicates that there could be many different sampling designs by which Distribution 1 could be sampled. It is apparent, however, that there are only five plot sizes which require a sample of less than 15 per cent of the total area (about five acres) to give an estimate of the average basal area such that the chances would be 2:1 that the estimate would be within 10 per cent of the true average. These plot sizes when applied according to the designs suggested in Table V would sample Distribution 1 with the desired precision.

The usefulness of the 10 × 20m and the 20 × 20m plot is severely limited because setting these plots out in a random manner would entail considerable difficulty in most stands. The same might be said of the long narrow plots; however, it is possible to use long (of indeterminate length) narrow plots in a random sampling design that can be easily and efficiently applied under field conditions (Schumacher and Chapman 1948, proportional sampling of blocks of diverse, but unknown, areas.).

TABLE V. *Plot sizes that would require samples of less than 15% of the total area to give estimates within ± 10% of the true average of basal area for Distribution 1 (Probability 2 : 1)*

| Plot size | Number of plots | Per cent of total area sampled |
|---|---|---|
| 10 x 20 m (A & B)... | 14 | 14 |
| 20 x 20 m..... | 7 | 14 |
| 4 x 140 m (B)..... | 5 | 14 |
| 10 x 70 m (A)..... | 4 | 14 |
| 10 x 140 m (A & B).. | 2 | 14 |

In spite of the above mentioned facts, all of these sampling designs would be adequate to sample Distribution 1 over this area with the desired precision. Which one the sampler uses is left largely to his choice.

However, there is a way by which the per cent of total area sampled can be reduced. It is a well-known fact that when using a long narrow plot, short segments, usually no longer than the width of the plot, can be systematically omitted without greatly impairing the efficiency of the plot (Hasel 1938, Table 9).

Thus, the 4 × 140m plot could be a line of eighteen 4 × 4m ultimate units spaced 4 meters apart. The 10 × 70m could be four 10 × 10 m ultimate units spaced 10 meters apart. Finally, the 10 × 140m plot could be seven 10 × 10m ultimate units spaced 10 meters apart. These plots with the segments omitted enable a sample of about 7% to give almost the same accuracy as a 14% sample without the segments omitted.

It is obvious that after omitting segments, four sampling designs—4 × 140m (B), 10 × 70m (A), 10 × 140m (B), and 10 × 140m (A)—would be the best to use, mainly due to the reduction in work following the reduction in area to be sampled.

The question then arises how would these same designs sample Distribution 2 over the same area?

By using the number of plots (in terms of the 2 × 2m) mentioned in Table V for each of the three plot sizes, in combination with the Distribution 2 variances for these same plot sizes (Fig. 4), the bounds can be determined within which the estimate of the mean of Distribution 2 will fall when the sampling designs best suited to sample Distribution 1 are applied to Distribution 2.

$$\frac{V(y)\ dist.\ 2}{^{n}dist.\ 1} = V(\bar{y})\ dist.\ 2$$

$$\frac{\sqrt{V(\bar{y})\ dist.\ 2} \times 100}{y\ Dist.\ 2} = \begin{array}{l}percentage\ of\ the\ true\ mean\ (\bar{y}),\ within\\ which\ the\ sample\ mean\ will\ fall\ (chances\\ 2{:}1).\end{array}$$

Upon making this determination, the results in Table VI were obtained. The table shows that, although each of the sampling designs sampled Distribution 1 with the same accuracy, there is a marked difference in their ability to sample Distribution 2. The two designs with plots running in Direction B show a greater accuracy than those that run in Direction A. This point serves to emphasize the fact that when one is interested in gaining a fairly accurate estimate of the less important vegetation, the longitudinal axis of the plot should cross any noticeable contour, soil, or vegetational banding within the community.

From all of the foregoing, it may be concluded that plot sizes 4 × 140m (B) and 10 × 140m (B) will give the best estimate of the total tree vegetation on the area (in terms of basal area).

TABLE VI. *Sampling precision obtained when the best sampling designs suited to Distribution 1 are used to sample Distribution 2*

| Plot size | Number of plots | Per cent of the total | Chances 2:1 that the sample mean will be within the following per cent of the true mean | |
|---|---|---|---|---|
| | | | Dist. 1 | Dist. 2 |
| 4 x 140 m (B). ... | 5 | 14 | ±10 | ±26 |
| 10 x 70 m (A).. ... | 4 | 14 | ±10 | ±48 |
| 10 x 140 m (B)..... | 2 | 14 | ±10 | ±30 |
| 10 x 140 m (A)..... | 2 | 14 | ±10 | ±59 |

One final point is that, apparently, estimates of the mean basal area of any individual species making up 10 per cent or less of the total basal area of the stand would be, at most, within only 25 or 30 per cent of its true mean. In other words, the sample that gives accurate information about the whole, may not give very accurate information about the individual

species making up a relatively small part of the whole (10% or less).

*The random sample*

All recommendations made previous to this point concerning plot shape, plot size, and number of plots are most useful when a random sample is employed. By random sample it is meant that every single variate of a population is regarded as having an equal and independent chance of being drawn. When one is drawn, whatever its error, it indicates nothing concerning the error of any succeeding observation drawn under the same conditions (Schumacher and Chapman 1948).

The use of the random sample has two important features. First, data gathered in this way can be treated statistically and their variance can be calculated. This, in itself, can give the sampler the assurance that his sample has a certain precision. Also, it is probable that the statistical approach will give new ways in which to evaluate vegetation. When and if such new methods arise they could be applied immediately to any data that had been gathered previously by random sampling methods. Secondly, the random sample eliminates personal bias, which is apt to be present in some "systematic" samples. This is of importance even when the data are not treated statistically. For example, one sampler may be prone to sample what he considers the richest or best developed portion of the stand. Another sampler may sample the stand as it happens to lie before him. Now, if each of them sampled the same stand, the first sampler would probably obtain an exaggerated estimate of basal area and an overestimated importance of certain species. Thus, these two estimates of the same stand would not be comparable. This might be carried further in saying that comparisons of any two stands measured by subjective methods would be of questionable value.

This does not imply that the recognition of the over-all features of the stand could be replaced by some quantitative statistical method. On the contrary, the classification of the community rests on personal judgment based on personal experience. But this is no reason why the stand or concrete community, once delimited, cannot be statistically sampled.

The greatest usefulness of the random sample, apparently, would lie in studies concerned with the correlation of environmental factors with the stand in which they were observed. Here, a precise estimate of what the stand contained would be desirable.

However, in phytosociology the need of a *precise* estimate of, for instance, basal area might be doubtful. But, regardless of the precision desired in community sampling, certain procedures made evident by this study should be followed in order to enhance the value of the sample.

They are: 1. Some form of rectangular plot should be used; 2. The longest axis of this plot should cross any observed contour, soil, or vegetational banding; and 3. The number of plots generally employed should be increased. The number will of necessity vary with the individual stand and the sampling precision desired. In this particular community, 32 randomly distributed 10 × 10m plots would be required to sample within ±10 per cent of the true mean (2:1 precision).

## Summary

1. A method is described whereby statistical variance can be used to determine the most favorable size and shape of plot to sample a natural plant population.
2. This method was applied to an immature oak-hickory forest in the North Carolina Piedmont.
3. Statistical variance was further used to determine the number of plots necessary to obtain a sample within definite limits about the true mean of the population.

4. The following results were obtained:
   a. When calculated on a unit-area basis, variance decreases as the plots are increased in length provided that the longest axes of the rectangular plots cross observed contours and vegetational or soil banding.
   b. The 4 × 140m and the 10 × 140m plot give the best estimate of the total tree vegetation on the sampled area in terms of basal area. Fourteen per cent of the total area must be sampled to obtain an estimate of the total basal area that will be within ±10 per cent of the true mean. However by systematically omitting segments no longer than the width of each plot, the sample size can be reduced to approximately 7 per cent without greatly impairing the precision of the sample.
   c. A sample that may give accurate information about the dominant tree vegetation may not give very accurate information about the lesser tree vegetation.
5. From this study it may be inferred that in phytosociological sampling the following procedures should be followed:
   a. Some form of rectangular plot should be used.
   b. The longest axis of the plot should cross any observed contour, soil, or vegetational banding.
   c. Samples should be laid out in a random manner to eliminate personal bias and to allow the data collected to be treated statistically, if desired.
   d. The number of plots now generally employed should be increased. The number will of necessity vary with the individual stand and the sampling precision desired.

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# THE EFFECT OF POPULATION DENSITY ON THE GROWTH OF AN ANIMAL POPULATION[1]

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## INTRODUCTION

1. It is well known that when an animal population grows in a spatially limited environment, the density of population exerts an influence upon the growing process or mode of population, which is characterized by the conditions and animals used in the particular experiment concerned. While many investigations have hitherto been made experimentally regarding the effect of population density upon various biological aspects with a number of important and interesting results, many problems still remain unresolved, especially with respect to the quantitative or theoretical interpretation of these results. In the present paper, we are concerned with a theoretical consideration of the density effect upon the mode of reproduction in a population under some simple assumptions in the hope of obtaining a consistent interpretation of existing experimental data on this subject.

The theory is developed assuming the well-known logistic growth equation for the mathematical form of the growing process of the population concerned, and the results thus obtained are compared with experimental data on some insect populations, in which case, however, the data obtained by one of the present authors on the population of the azuki bean weevil, *Callosobruchus chinensis* (Utida 1941a, 1941b, 1942) are mainly employed because of the detailed information that they provide. However, we hope that the theory described in this paper will be examined by comparing it with many experimental data on the populations of many other animals.

## DENSITY EFFECT ON RATE OF REPRODUCTION (I)

2. Consider the growth of an animal population in a constant environment starting with $\frac{1}{2} N_0$ pairs of adult individuals. Initial population density $N_0$ is usually adopted as a measure by means of which to express quantitatively the effect of density upon the growth of a population. We shall follow this convention in the subsequent theoretical treatment. In order to develop a theoretical analysis of any population problem, it is first necessary to assume a relevant mathematical expression for the growth of the population concerned. In this paper, following the usual treatment hitherto attempted in population dynamics, we shall assume the well-known logistic equation as the basis of our theory, which may be written as:

$$N(t) = \frac{\epsilon/h}{1 + \{(\epsilon/hN_0) - 1\} e^{-\epsilon t}}, \qquad (1)$$

where $N(t)$ is the number of individuals present in the environment at any time $t$ after the beginning of breeding, $\epsilon$ is the intrinsic rate of reproduction of the animal, and $h$ is the Pearl-Verhulst coefficient for the system concerned. Putting $N(t) = N_\tau$ where $\tau$ is the interval of one generation time, equation (1) becomes

$$N_\tau = \frac{\epsilon/h}{1 + \{(\epsilon/hN_0) - 1\} e^{-\epsilon\tau}}. \qquad (2)$$

It would be expected that some of the individuals introduced initially in the container may die during the course of

[1] Contribution from the Department of Fisheries, Kyoto University.
Contributions from the Entomological Laboratory, Kyoto University, No. 214.

growth. Therefore, the number of living individuals that would be found at the end of one generation may, in general, be represented to a first approximation by $N_\tau - \sigma N_0$ with $\sigma$ being the average mortality of adult animals in one generation. The value of $\sigma$ is necessarily $0 \leqq \sigma \leqq 1$. Thus, we may define the apparent rate of reproduction, $R$, or the number of progeny individuals produced per parent female, by

$$R = \frac{N_\tau - \sigma N_0}{\frac{1}{2} N_0}. \qquad (3)$$

The reason why $R$ is termed "apparent" is due to the expectation that the individuals of $N_\tau - \sigma N_0$ may include not only the newly emerged adults but also surviving individuals of the parent generation. The true rate of reproduction, $R'$, is given by $\frac{N_\tau - N_0}{\frac{1}{2} N_0}$. However, the mean rate of reproduction which is empirically obtainable with usual procedures is not $R'$ but $R$, since it is practically very difficult to distinguish between newly emerged and surviving adults. The quantity $\sigma$ will generally depend not only on the kind of animals and the environmental conditions but also on the initial density of population. That is, we should expect a density effect on $\sigma$. In the present paper, however, this density effect is ignored for mathematical simplicity, and we shall treat $\sigma$ as a parameter intrinsic to the system concerned. The reason for setting this simplified assumption stems from the fact that the literature is not yet rich in data suited for exact quantitative discussion of the density dependence of $\sigma$. Fortunately, for the data on the population of the azuki bean weevil with which our theory will mainly be compared, the condition that $\sigma = 1$ is found to hold for all values of $N_0$ investigated, thus removing ambiguity resulting from neglect of the density effect on $\sigma$. Obviously, neither $\epsilon$ nor $h$ depends on $N_0$, so that both quantities defined by

$$b \equiv e^{-\epsilon\tau}, \quad c \equiv \frac{(1 - b)h}{\epsilon}$$

are also regarded as constants not dependent on $N_0$. Taking this fact into account, an explicit relation between $R$ and $N_0$ is obtained from equations (2) and (3) in the form:

$$R = 2\left(\frac{1}{b + cN_0} - \sigma\right), \qquad (4)$$

which indicates a hyperbolic change of $R$ with change in $N_0$. A similar equation to this was already presented by Terao (1929) and by Miner (1932) on the basis of the logistic growth equation using somewhat different procedures from our own, although some ambiguous points are found to be involved in their treatments. Farr's equation that $R = \alpha N_0{}^\beta$ ($\alpha$ and $\beta$ are both constants) has frequently been employed for describing experimental data, but this is apparently an empirical one, so that constants $\alpha$ and $\beta$ cannot possess any concrete biological significance. On the contrary, parameters $b$, $c$ and $\sigma$ in our equation (4) consist only of quantities having definite biological meanings. Thus, on fitting equation (4) to experimental data, it is possible to determine the actually significant values of $\epsilon$ and $h$ which are the parameters of fundamental importance for describing the logistic population concerned.

In his study on the experimental population of the azuki bean weevil, Utida (1941a) analyzed the data by making use of Farr's equation, confronting a difficulty in which three different sets of values had to be assigned to constants $\alpha$ and $\beta$ while the range of $N_0$ was changed. A similar difficulty was also reached by MacLagan (1932) in the experimental population of the granary weevil, *Calandra granaria*. However, it can be shown that such difficulties do not arise when

analysis of data is made on the basis of our equation (4). To demonstrate this, we put equation (4) in the form:

$$\frac{1}{R+2\sigma} = \frac{b}{2} + \frac{c}{2}N_0, \qquad (5)$$

which suggests a linear relation between $1/(R + 2\sigma)$ and $N_0$. Figure 1 shows how well this linear relation is followed

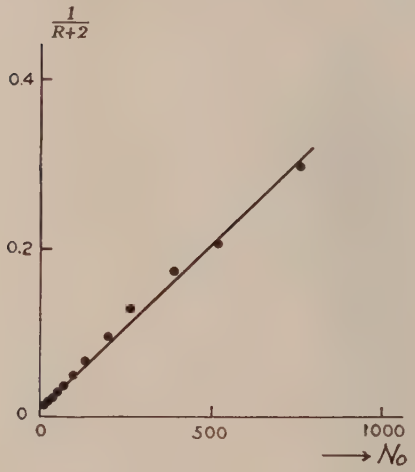


FIG. 1. Linear relation between $1/(R+2)$ and $N_0$, where $R$ is the mean rate of reproduction and $N_0$ is the initial population size.

by the data for the azuki bean weevil population (Utida 1941a), where $\sigma$ has been taken to be unity in accordance with the experimental information. From the slope and the intercept on the ordinate axis of the straight line drawn on the figure, the values of $b$ and $c$ are determined:

$$b = 0.024,\ c = 0.0008.$$

Substituting these values into equation (4) and taking $\sigma = 1$ for this population, we have

$$R = \frac{2500}{N_0 + 30} - 2, \qquad (6)$$

whence $R$ is plotted against $N_0$ and compared with the corresponding experimental values (Fig. 2). Agreement between theory and experiment may be regarded as satisfactory. Here, it is important to note that so good a fit to our equation (4) has been attained using a single set of values for parameters $b$, $c$ and $\sigma$. Further checks of the applicability of equation (4) are given in Figure 3, where experimental data on some insect species, such as the fruit fly *Drosophila melanogaster*, the confused flour beetle *Tribolium confusum*, and some parasitic wasps, *Trichogramma evanescens*, *Heterospilus prosopidis*, and *Neocatolaccus mamezophagus*, are quoted from the literature and compared with the theory, the value of $\sigma$ taken in each case being indicated in the legend.

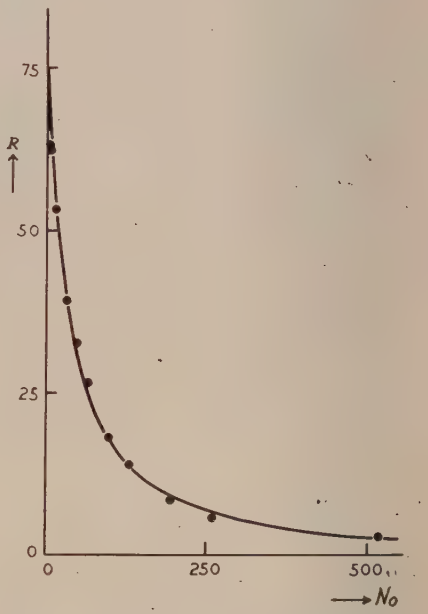


FIG. 2. Density effect on the mean rate of reproduction, $R$; points: experimental; line: theoretical (Eq. (6)).

3. Next, we shall examine the effect of density of the parent population on the total number of living individuals found after the lapse of one generation time. This is to investigate the density effect on the growth of a population itself. The total number of living individuals at time $\tau$, which is hereafter designated by $P$, is evidently given by $N_\tau - \sigma N_0$, for which an expression in terms of $N_0$ is

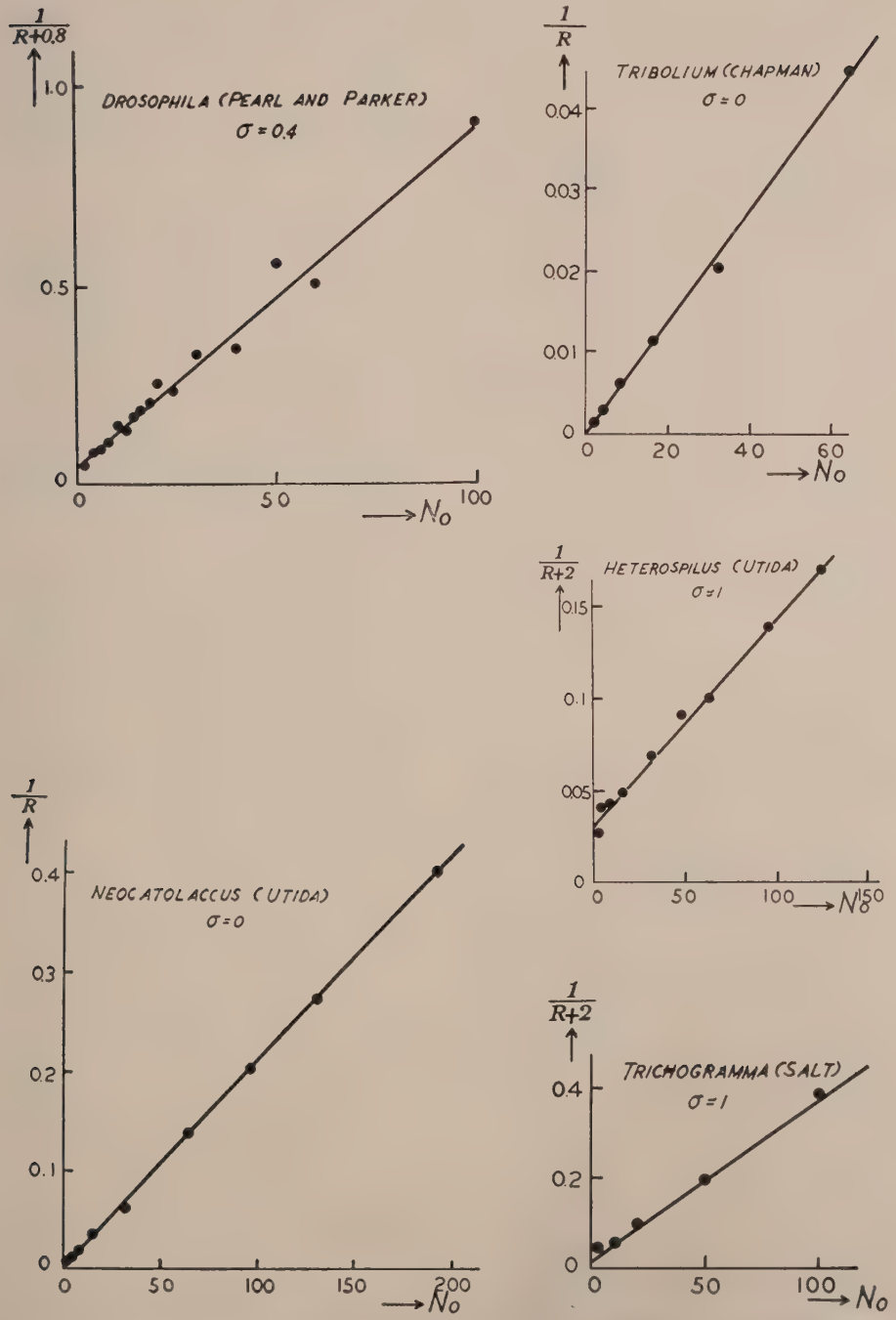


FIG. 3. Experimental checks of Eq. (5); data are due, respectively, to Chapman (1928), Pearl and Parker (1922), Salt (1936), and Utida (1944 a, b).

readily obtained from equations (3) and (4) as:

$$P = N_0 \left( \frac{1}{b + cN_0} - \sigma \right). \qquad (7)$$

For the case of the azuki bean weevil population to which we have referred above, this equation is written numerically as:

$$P = N_0 \left( \frac{1250}{N_0 + 30} - 1 \right), \qquad (8)$$

from which $P$ is plotted against $N_0$ as shown in Figure 4. On this figure, the

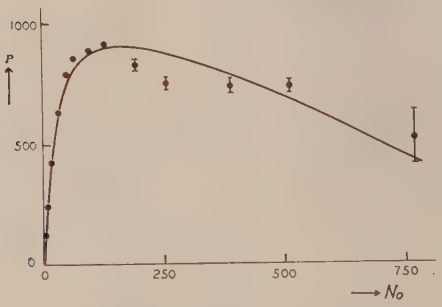


FIG. 4. Density effect on the total population of the progeny generation, $P$; points: experimental; line: theoretical (Eq. (8)).

corresponding experimental values are plotted for comparison with black circles. Agreement between theory and experiment is again satisfactory, especially in the initial stages of increase in $P$. One of the interesting facts which can be seen from this figure is the presence of a point at which $P$ attains a maximum value. This implies that there exists an optimum density of parent population for the increase of the total population. Experimental evidence of this fact was first found by Utida (1941a) in the azuki bean weevil population, data of which have been plotted in Figure 4, and its biological significance has since been emphasized on many occasions (Utida 1949, 1950). Similar results showing the presence of an optimum density have recently been demonstrated by Chiang and Hodson (1950) and by Nicholson (1950) in experimental populations of some insect species.

When $\sigma = 0$, or no parent individual dies in a generation, equation (7) takes the form:

$$P = \frac{N_0}{b + cN_0} \qquad (9)$$

This equation gives a plot which, with increase in $N_0$, increases monotonically and approaches $1/c$, thus revealing no maximum point. It is furthermore easily shown that when either $b = 0$ or $c = 0$, equation (4) also provides a curve with no maximum point. Thus it is concluded that occurrence of the optimum density in the relation between $P$ and $N_0$ is possible only in cases where the condition $bc\sigma \neq 0$ is satisfied.

4. Discussions given in previous sections have been confined to the population growth in a generation. In the present section, considerations are extended to successive generations to obtain information on the population changes from generation to generation.

Applying the treatment described in section 3 to the interval from the $(n\text{-}1)$th generation to the $n$th generation, we obtain the following relation:

$$P_n = P_{n-1} \left( \frac{1}{b + c\,P_{n-1}} - \sigma \right), \qquad (10)$$

where $P_n$ $(n \geqq 1)$ denotes the number of living individuals present in the environment after the lapse of $n$ generations. Equation (10) is a nonlinear difference equation, from which the change of population in successive generations can be followed as a function of generation number $n$ with any given initial density of population $P_0 (\equiv N_0)$. Due to its nonlinearity, however, it appears to be hopeless at present to derive the general solution of equation (10). For this reason, we must be satisfied with inspecting only a part of the behavior of the general solution by making use of an appropriate numerical method. How-

ever, it can be shown that in special cases where $bc\sigma = 0$ holds, the above equation can be solved analytically, and thus discussions of the problem can be made quite general. Now, we shall examine the nature of the solution of equation (10) somewhat in detail.

(i) We shall at first consider the problem under the condition that $\sigma \neq 0$. In the special case where $b = 0$ but $c \neq 0$, equation (10) is solved to give

$$P_n = \begin{cases} N_0 \, (n = 2m), \\ \dfrac{1}{c} - \sigma N_0 \, (n = 2m + 1), \end{cases} \tag{11}$$

where $m = 0, 1, 2, \ldots$. Solution (11) gives the curve represented graphically in Figure 5 as A, oscillating with a constant amplitude up and down about the central line which is given by $P_n = \dfrac{1}{2}\left[\dfrac{1}{c} + (1 - \sigma) N_0\right]$. Apparently, this resembles the oscillation observed by Park and Frank (1950) in the experimental population of *Tribolium confusum*. However, such a non-damped oscillation would not be realized biologically since the condition that $b = 0$ corresponds to $\epsilon = \infty$ or $\tau = \infty$, which is evidently impossible in practice. It is, however, supposed that the oscillatory process here shown may occur approximately in populations in which the parameter $\epsilon$, the intrinsic rate of reproduction, is sufficiently large.

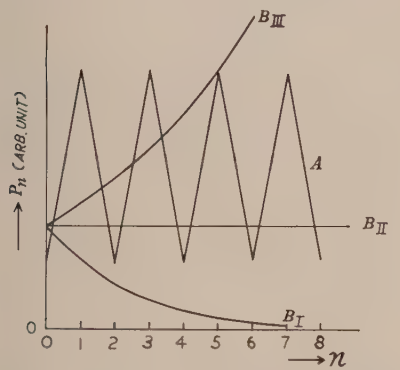


FIG. 5. Theoretical modes of population change in successive generations, when (A) $\sigma \neq 0$, $b = 0$, $c \neq 0$; or (B) $\sigma \neq 0$, $b \neq 0$, $c = 0$.

Next, we shall consider the case where $b \neq 0$ but $c = 0$. The condition that $c = 0$ corresponds to $h = 0$, as is known immediately from the definition identity of $c$. As was shown by Fujita (1951), when the process of population growth is logistic, the condition $h = 0$ is realized in spatially unlimited space. In this particular case, equation (10) is solved analytically and we have

$$P_n = N_0 \left(\frac{1}{b} - \sigma\right)^n \tag{12}$$

We now have the condition that $0 < b \leqq 1$, since $b \equiv e^{-\epsilon\tau}$ and since $b \neq 0$ by assumption. Also we have $0 < \sigma \leqq 1$ since $0 \leqq \sigma \leqq 1$ and since the case $\sigma \neq 0$ is here being considered. Thus, the following three cases can now be considered: $0 \leqq \dfrac{1}{b} - \sigma < 1$, $\dfrac{1}{b} - \sigma = 1$, $1 < \dfrac{1}{b} - \sigma < \infty$. The plots of solution (12) corresponding to these three cases are shown in Figure 5 as $B_I$, $B_{II}$, and $B_{III}$, respectively. It is seen that the plots thus obtained give neither oscillation nor a maximum point.

Finally, the most general case in which $bc\sigma \neq 0$ will be considered. In this case, as mentioned above, the analytical solution of equation (10) is impossible to obtain, and we shall be satisfied with discussing the problem by a numerical method. For this purpose, we shall take the following numerical example:

$$b = 0.024, \quad c = 0.0008, \quad \sigma = 1,$$

which are the values determined in section 2 by fitting the theory therein described to the experimental data on the azuki bean weevil population. Substituting these numerical values into equation (10) and taking $N_0 = 2$, successive change in $P_n$ with change in $n$ has been computed in a straightforward manner,

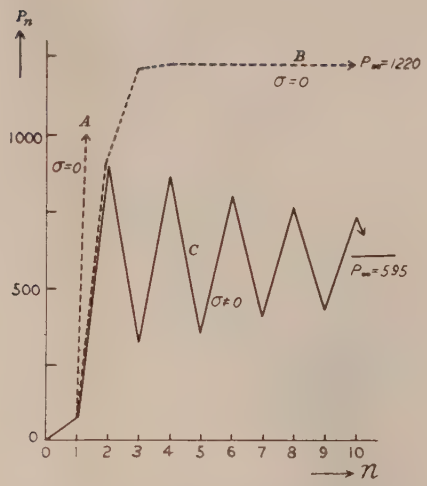


FIG. 6. Theoretical modes of population change in successive generations, when (A) $\sigma = 0$, $b \neq 0$, $c = 0$; (B) $\sigma = 0$, $b \neq 0$, $c \neq 0$; (C) $\sigma \neq 0$, $b \neq 0$, $c \neq 0$.

resulting in the plot shown in Figure 6 as a solid line. With progressively increasing $n$, $P_n$ initially increases monotonically[2] and then enters the state of damped oscillation which converges to a limiting value $\equiv P\infty = 595$ as $n \to \infty$ It can be shown directly from equation (10) that this limiting value of $P_n$ is generally given by $\frac{1}{c}\left(\frac{1}{1+\sigma} - b\right)$, which also represents the equilibrium state of a system in which $b\,c\,\sigma \neq 0$. The damped oscillation described here has already been demonstrated in the experimental population of the azuki bean weevil (Utida 1941b). The amplitude and the damping rate in the oscillation generally depend on the values of $b$, $c$, $\sigma$ and $N_0$. However, detailed information on this subject may be impossible to obtain in the absence of an analytical solution of equation (10).

(ii) We shall next discuss the case in which $\sigma = 0$. In this case, equation (10) reduces to

$$P_n = \frac{P_{n-1}}{b + c\,P_{n-1}} \qquad (13)$$

The analytical solution of this nonlinear difference equation can be obtained to give[3]

$$P_n = \frac{1 - b}{c - b^n\left(c - \frac{1 - b}{N_0}\right)} \qquad (14)$$

which reduces, when $b \neq 0$ and $c = 0$, to

$$P_n = \frac{N_0}{b^n}. \qquad (15)$$

When $b = 0$ and $c \neq 0$, there exists no solution subject to the given initial condition $P_0 = N_0$ if, moreover, the condition that $1/c = N_0$ be not satisfied. The nature of the curves given by solution (15) is self-evident since $b$ is now subjected to the condition that $0 < b \leq 1$; generally, it gives a plot monotonically increasing to infinity as $n$ is increased indefinitely. An example of such a plot is shown in Figure 6 with a dotted line A, in evaluation of which the same $b$ value as used in (i) has been adopted for comparison. On the other hand, solution (14) is shown to converge to a finite value $\frac{1}{c}(1 - b)$ when $n$ is increased indefinitely. Curve B in Figure 6 is a numerical example of solution (14), in evaluation of which the same $b$, $c$ and $N_0$ values as used in (i) have again been employed for the sake of comparison. It should be noted here that the curve B thus evaluated has a similar appearance to the well-known logistic curve.

Summarizing all of the results obtained above for the modes of population change in successive generations, we can construct Table I.

As is evident from the tabular summary given in Table I, the condition that

[2] In some cases, a monotonically decreasing plot will be obtained according to the combination of numerical values of $b$, $c$, $\sigma$ and $N_0$.

[3] For this solution we are indebted to Professor Y. Komatsu at the Department of Mathematics of the Tokyo Institute of Technology.

TABLE I. *Summary of the results derived from equation (10)*

| | $\sigma=0$ | $\sigma\neq0$ |
|---|---|---|
| $b=0$ $c\neq0$ | Equation (10) is soluble only when $c=1/N_0$. | Non-damping type of oscillation |
| $b\neq0$ $c=0$ | Monotonic, non-decreasing type; $P_\infty=\infty$ in general | Monotonic increasing or decreasing type |
| $b\neq0$ $c\neq0$ | Monotonic increasing or decreasing type, having a point of saturation; $P_\infty=\frac{1}{c}(1-b)$ | Damping type of oscillation; equilibrium point is given by $P_\infty=\frac{1}{c}\left(\frac{1}{1+\sigma}-b\right)$ |

$\sigma \neq 0$ is necessary in order that oscillatory type of population change be produced; whether or not the oscillation is damped is dependent on $b$. These theoretical demonstrations are believed to be among the most important results revealed in the present study. Analysis developed above for the modes of population change in successive generations is apparently of qualitative character, so that in order to obtain quantitative information, more extensive mathematical study needs to be devoted to the solution of equation (10). At the same time, experimental checks on the validity of our theoretical results summarized in Table I are urgently needed.

## DENSITY EFFECT ON RATE OF REPRODUCTION (II)

5. In previous sections, we have considered how the population density affects the average rate of reproduction when it is controlled by changing the number of individuals liberated in a container of a constant volume. Since the density of population is defined as the ratio of individual numbers to the volume of the environment wherein the animals live, the same density effect should also be expected to occur when the population density is controlled by changing the container volume with a fixed number of individuals liberated therein. If this prediction were not realized, the conception of density effect would fail. The theory, if it is correctly established, should yield an equally exact interpretation of the density effect, whether the number of individuals is changed in an environment of constant volume or a constant number of individuals is liberated in environments of different volumes. In this section, by limiting consideration to the apparent rate of reproduction $R$, we shall see whether our theory described above has been so constructed as to satisfy this postulate.

It was proved by Fujita (1951) that when population growth is governed by the logistic law, the volume of environment $V$ (probably, that available for the population) is connected with the Pearl-Verhulst coefficient, $h$, by the relation:

$$h = \frac{1}{kV}, \tag{16}$$

where $k$ is a proportionality constant independent of $N_0$ and $\epsilon$, at least to a first approximation. Thus, if we define quantities $a$ and $b$ as

$$a \equiv \epsilon\, k, \quad b \equiv e^{-\epsilon\tau}$$

we can obtain the following equation from equations (2) and (16):

$$N_\tau = \frac{N_0}{\left(\frac{1-b}{a}\right)\left(\frac{N_0}{V}\right)+b}, \tag{17}$$

which may moreover be put in the form:

$$\frac{N_0}{N_\tau}=\left(\frac{1-b}{a}\right)\left(\frac{N_0}{V}\right)+b. \tag{18}$$

This equation shows that a linear relation should hold between $N_0/N_\tau$ and $N_0/V$, the latter being nothing but the population density in the strict sense. Utida (1942) obtained experimentally the relation between $N_\tau - \sigma N_0$ and $V$ as a function of parameter $N_0$ in the experimental population of the azuki bean weevil. From the data therein presented, numerical values of $N_0/N_\tau$ and $N_0/V$

have been computed, taking $\sigma = 1$ for the population of this insect as has been stated previously, and the resultant numerical values are plotted in Figure 7. It

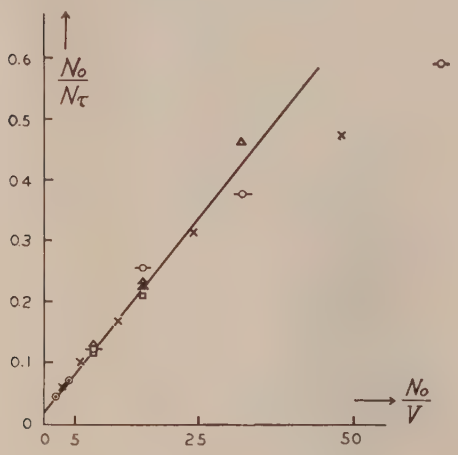


FIG. 7. Linear relation between $N_0/N_\tau$ and $N_0/V$, where $V$ is the volume of container; points: experimental.

will be seen that the plotted points fall on a straight line as should be expected from equation (18), except for two points corresponding to higher densities. The reason for these deviations is not clear, but it is possible that under such intense crowding a different growth process, not describable by the logistic law, may supervene. The straight line on Figure 7 provides the numerical values of $a$ and $b$ in equation (17), which are

$$a = 75.4, \quad b = 0.020.$$

Introducing these values into equation (17) and making some rearrangement of the resultant equation, we obtain the expression for the apparent rate of reproduction in the form:

$$R = \left\{ \frac{1000}{20 + 13\left(\frac{N_0}{V}\right)} - 1 \right\}, \quad (19)$$

where $\sigma$ has again been taken to be unity. From this equation, $R$ has been computed as a function of $V$ for several given values of $\frac{1}{2} N_0$, i.e., the pairs of weevils liberated initially, and the results are plotted in Figure 8 by solid lines. In this figure,

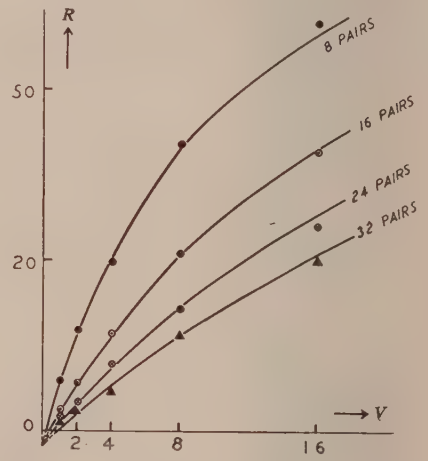


FIG. 8. The effect of the volume of container, $V$, on the mean rate of reproduction, $R$; points: experimental; lines: theoretical (Eq. (19)).

the corresponding experimental data from Utida's original paper (1942) are plotted for comparison. Over almost all ranges of $V$ and $N_0$ plotted, it is seen that our theoretical curves follow the experimental values rather closely. This result indicates that our theory is also soundly applicable to data obtained in cases where the population density is controlled by changing the volume of environment, keeping the number of individuals introduced therein at constant value. Thus the theory developed in the present paper indeed provides a consistent explanation of the density effect on reproduction irrespective of the way in which the density of population is manipulated.

## SUMMARY

With the purpose of obtaining a theoretical basis on which existing experimental data on the density effect upon reproduction may be interpreted consistently, a mathematical analysis has been developed from the well-known logistic growth equation. Consideration has first been given to the growth process occur-

ring in the interval of one generation time, resulting in mathematical relations for the effects of initial population density $N_0$ on (1) the apparent rate of reproduction, $R$, and (2) the total number of living individuals, $P$, to be found at the end of the generation. These are given in equations (4) and (7), respectively. Experimental checks on these equations have been made, using the data which had been presented by Utida (1941a) on an experimental population of the azuki bean weevil, although data from some other insect populations have also been used to confirm equation (4). Satisfactory agreements of these equations with the corresponding experimental data are shown graphically in Figures 1, 2, 3 and 4. One of the interesting facts thereby revealed is the clear evidence of a density of parent population at which the total population reaches a maximum value. Experimental proof of the existence of such an optimum density in population growth had previously been given by the populations of several insect species, but its theoretical foundation has remained obscure.

Next, equation (7) has been modified to give a mathematical relation for describing the population changes from generation to generation. This relation is given in equation (10). By solving this analytically, if possible, or numerically, it has been shown that, theoretically, population changes in successive generations should follow one of the various modes indicated in Table I. Some experimental data that meet this theoretical requirement have been mentioned.

Finally, employing a relation which has recently been derived by Fujita between the volume of environment and the Pearl-Verhulst coefficient, the logistic equation (3) has been transformed into equation (18), and it has been demonstrated that this equation is also well fitted by the experimental data on the azuki bean weevil population (Utida 1942), in which the density effect on reproduction was studied by changing the volume of the container. The agreements thus obtained are found in Figures 7 and 8.

The authors wish to express their hearty gratitude to Professor Y. Komatsu at the Department of Mathematics of the Tokyo Institute of Technology for his help in suggesting the exact solution of equation (13).

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# A TEST OF RANDOM VERSUS SYSTEMATIC ECOLOGICAL SAMPLING

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## INTRODUCTION

Of the numerous published papers pertaining to ecological sampling, most are concerned with the size, shape, and number of plots making the most efficient sample, or yielding the greatest precision for the minimum of work. The problem has been attacked empirically, by use of the species-area curve (Cain 1938) or by statistical methods (Clapham 1932, Ashby 1935, Pechanec and Stewart 1940, Penfound 1945, and others).

The present investigation is of quite a different nature in that it compares a systematic sample, commonly used by ecologists, with a random sample, required by statisticians, as obtained in a completely enumerated forest stand.

When ecologists have to analyze the vegetation of a forest stand, many take 10 to 20 quadrats of 10 meters per side, evenly distributed along evenly spaced lines, a pattern which constitutes, if properly done, a systematic sample. This kind of sample is preferred for its easy applicability in the field. It is also believed to be more likely to include the variations of the stand, and thus to be more accurate, than any scheme of random sampling. In fact, this has been proved in certain instances (Hasel 1938, Finney 1948).

However, Finney (1949) has shown that, when there is a strongly marked pattern of variation over the stand, this might not be true. If that pattern is periodic, systematic sampling can be considerably less accurate than some kinds of random sampling.

Additionally, the major draw-back of systematic sampling is that it does not offer in itself the basis for the assessment of error. Statistical treatment of sampling data leading to estimates of error is necessarily based on the assumption that all sampling units have been chosen independently and at random. It it thoroughly unsound to assess the error from the different sampling plots of a systematic set where the position of all other plots is determined by the location of the first one.

If, in the field of ecology, there is a need for reliable quantitative data on the composition of plant communities, whether it be fundamental or applied studies, then any estimate of a population mean should be substantiated by the estimate of its error, even if some fraction of the accuracy might be lost.

How much of this accuracy will be lost, if any, by substituting randomization for systematic sampling is a question to which no standard answer can be given. It all depends on the nature of the variation over the stand.

Some studies have been made in timber surveys on extensive areas, where the smallest plot was sometimes larger than a whole stand used by an ecologist as representative of a community and where the only variable sampled was the total timber volume. For such a study, Hasel (1938) concluded that the variance for the systematic sampling was about half that of the stratified random sampling. Finney (1948) found in two forests a smaller variance in systematic than in random sampling, but, in another survey (1949) the latter was substantially more

[1] Thanks are due to Professor H. J. Oosting who suggested and supervised this study, and to Professor F. X. Schumacher for checking the statistical work. Special acknowledgment is due to F. H. Bormann who made his data available.

accurate at certain intensities because the variation over the stand was periodic.

Similar investigations have not been made in ecological sampling where one commonly deals with rather small stands, and, rather than total volume, more detailed measurements of density and basal area for the whole population and also for each species.

It seemed desirable to compare random and systematic sampling for ecological purposes. The objective of this project is to make such a comparison, using a modification of Finney's and Hasel's methods.

The data used here come from Bormann's (1953) complete enumeration of a five-acre oak-hickory stand in Duke Forest. Since all woody plants above one inch d.b.h. had been measured and recorded for each of the 4,900 two by two meter squares represented on a 140m by 140m area, it was possible to map the stand on a 1 to 100 scale and to use the map for trying any kind of sampling procedure.

Statistical variances[2] will be used in determining the precisions of the different sampling schemes. Numerically, the precision, or amount of information, of a sample will be measured by the reciprocal of its variance and the efficiency of a form of sampling relative to another expressed as the ratio of their respective precisions (Finney 1948).

[2] The variance of the sample, expressed numerically as the average of the squares of the deviations of the observations around the sample mean, is a measure of dispersion among observations (Schumacher and Chapman 1948). Divided by the number of observations it gives the variance of the sample mean. The square root of the latter figure is the standard error of the sample mean, which indicates the limits around the sample mean between which the chances are two to one that the true population mean will fall.

If, at a specified intensity of sampling, a particular scheme shows a greater variance, and standard error, than another, the first one is less accurate since, for the same threshold of probability (2 to 1), the true population mean may fall in a wider range of values.

## Methods of Computing Variances

Variances have been calculated for three kinds of sampling: systematic, unrestricted random, and stratified random.

It was decided to use the 10 by 10 meter quadrat as a basic unit in sampling since it is commonly adopted by forest ecologists. Each quadrat is treated in the same manner as the strip unit in Hasel's and Finney's investigations.

The area of the stand, originally 140m × 140m, has been reduced to 120m × 120m, or 144 ten by ten meter quadrats for the sake of convenience in the calculations. Indeed, the number 144, being highly divisible, permits the variances to be calculated at the following intensities of sampling with no fraction of a set to be treated separately:

| 1 in r<br>$r$ | Per cent of total area |
|---|---|
| 3 | 33.33 |
| 4 | 25.00 |
| 6 | 16.66 |
| 8 | 12.50 |
| 9 | 11.11 |
| 12 | 8.33 |
| 16 | 6.25 |
| 18 | 5.55 |
| 24 | 4.17 |
| 36 | 2.77 |

### *Systematic sampling variances*

In a population composed of $N$ (144 in this case) sampling units, or quadrats, a series of $n$ quadrats distributed over the area to form the most regular pattern constitutes a systematic sample. The ratio of the area sampled to the total area $n/N=1/r$ determines the intensity of sampling (Figure 1).

As stated above, no valid estimate of variance can be assessed from the different observations of *one* systematic set.[3]

[3] It must be said, though, that under exacting specifications, practically never encountered, estimates have been made in that way by considering the population as a polynomial distribution (Cochran 1946, Delury

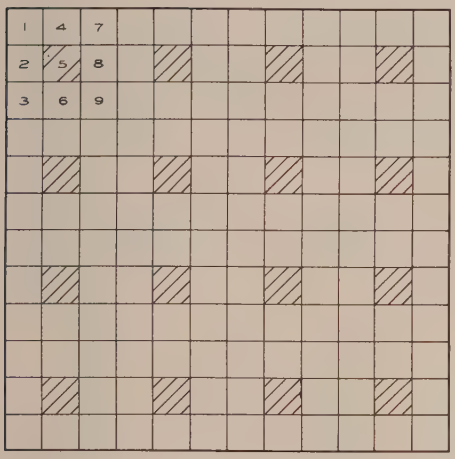


FIG. 1. Pattern of a systematic sample at an intensity of *1* in *9* (11.11% of the entire area). The sample is comprised of $\frac{N}{r} = \frac{144}{9} = 16$ quadrats. The entire area is covered by the 9 samples of 16 quadrats each, the first quadrat occupying successively the positions *1* — *9*.

But when data from complete enumerations are available, it is possible to estimate the variance of this type of sampling by forming the series of all possible one in $r$ samples with regular pattern and to calculate the variances of the members of this series, which covers exactly the whole area.

*Example:* see Figure 1, intensity of sampling 1 in 9, 9 possible samples. The sum of the squares of the deviations between the 9 totals divided by the number of degrees of freedom $(r - 1)$ gives an estimate of the variance of a sample of 16 quadrats of which the first one has been taken at random from the numbers 1 to 9.

For the sake of comparison, all variances are reduced to the unit area, *i.e.*, the 10 by 10 meter quadrat. In this particular case there are 9 samples of 16 quadrats giving 9 totals:

$$\sum_{S}^{9}\left[\binom{16}{S}\right] = \text{total population}$$

$$\frac{\sum_{S}^{9}\left[\binom{16}{S}\right]}{9} = \text{mean per sample} = \bar{S}$$

The sum of the squared deviations divided by the number of degrees of freedom

$$\frac{\sum_{S}^{9}\left[(S - \bar{S})^2\right]}{n - 1} = V\binom{16}{S}$$

Expressed in terms of unit area, the variances $= \frac{V\binom{16}{S}}{16}$.

This method, used by Hasel, has, according to Finney, the following disadvantage: the estimate of variance for a 1 in $r$ intensity of sampling is based on only $(r - 1)$ degrees of freedom. For high intensities, that is for small values of $r$, an estimate based on $(r - 1)$ degrees of freedom can scarcely be considered as reliable.

To meet this deficiency, Finney proposes to increase the number of degrees of freedom by breaking the whole series of sampling units (strips or quadrats) into smaller groups. "The variance may then be assessed for each group and later combined into an average value for the whole. The groups need not be independent, and may overlap without producing any bias in error estimation though the total number of degrees of freedom used in the calculation will not then be an indicator of the reliability of the result. . . . Care should be taken to choose a fairly symmetrical system of overlapping groups."

This is explained by the following numerical example. Consider a systematic sampling of the density of the total population at a sampling intensity of 1 in 9 (11.11 per cent of the total area). The 144 quadrats are numbered as indicated in Figure 2. Instead of taking the entire series of 144, as in Hasel's

1950), but, according to Finney, there is no mathematical proof of the suitability of such treatment. The calculations are involved and somewhat subjective.

method, the quadrats are arranged in smaller overlapping groups to form a fairly symmetrical system:

| 10 groups: | Group no. | Quadrat no. |
|---|---|---|
| | 1 | 1 - 45 |
| | 2 | 12 - 56 |
| | 3 | 23 - 67 |
| | 4 | 34 - 78 |
| | 5 | 45 - 89 |
| | 6 | 56 - 100 |
| | 7 | 67 - 111 |
| | 8 | 78 - 122 |
| | 9 | 89 - 133 |
| | 10 | 100 - 144 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 4 | 7 | 37 | 40 | 43 | 73 | 76 | 79 | 109 | 112 | 115 |
| 2 | 5 | 8 | 38 | 41 | 44 | 74 | 77 | 80 | 110 | 113 | 116 |
| 3 | 6 | 9 | 39 | 42 | 45 | 75 | 78 | 81 | 111 | 114 | 117 |
| 10 | 13 | 16 | 46 | 49 | 52 | 82 | 85 | 88 | 118 | 121 | 124 |
| 11 | 14 | 17 | 47 | 50 | 53 | 83 | 86 | 89 | 119 | 122 | 125 |
| 12 | 15 | 18 | 48 | 51 | 54 | 84 | 87 | 90 | 120 | 123 | 126 |
| 19 | 22 | 25 | 55 | 58 | 61 | 91 | 94 | 97 | 127 | 130 | 133 |
| 20 | 23 | 26 | 56 | 59 | 62 | 92 | 95 | 98 | 128 | 131 | 134 |
| 21 | 24 | 27 | 57 | 60 | 63 | 93 | 96 | 99 | 129 | 132 | 135 |
| 28 | 31 | 34 | 64 | 67 | 70 | 100 | 103 | 106 | 136 | 139 | 142 |
| 29 | 32 | 35 | 65 | 68 | 71 | 101 | 104 | 107 | 137 | 140 | 143 |
| 30 | 33 | 36 | 66 | 69 | 72 | 102 | 105 | 108 | 138 | 141 | 144 |

FIG. 2. The distribution of assigned quadrat numbers for the *1* in *9* intensity of sampling.

The first group (1 - 45) is composed of the following 9 possible samples:

| Quadrats no. | 1-10-19-28-37 | giving a sample sum of | 84 |
|---|---|---|---|
| | 2-11-20-29-38 | " " " " " | 84 |
| | 3-12-21-30-39 | " " " " " | 102 |
| | 4-13-22-31-40 | " " " " " | 109 |
| | 5-14-23-32-41 | " " " " " | 89 |
| | 6-15-24-33-42 | " " " " " | 105 |
| | 7-16-25-34-43 | " " " " " | 101 |
| | 8-17-26-35-44 | " " " " " | 108 |
| | 9-18-27-36-45 | " " " " " | 115 |

A sum of squares of deviations is then calculated for these 9 totals, the result being 1032 based on 8 degrees of freedom. The same calculations are repeated for each of the 10 series with the following results:

| Group | Totals of 5; groups of 45 Sums of squares |
|---|---|
| 1 - 45 | 1032 |
| 12 - 56 | 1008 |
| 23 - 67 | 946 |
| 34 - 78 | 482 |
| 45 - 89 | 1090 |
| 56 - 100 | 1338 |
| 67 - 111 | 704 |
| 78 - 122 | 670 |
| 89 - 133 | 566 |
| 100 - 144 | 736 |
| | 8572 |

Each group providing 8 degrees of freedom, we have now 80 degrees of freedom and the mean square will be $8572/80 = 107.15$. In each group, each sample is a sum of 5 quadrats. Hence, the variance per quadrat is $107.15/5 = 21.43$.

As Finney says: "This estimate is not as reliable as if it were based upon 80 *independent* degrees of freedom since the groups overlap. But it is certainly much better than an estimate based on eight degrees of freedom. . . . The choice of $k$, the number of units to include in each set, [which is 5 in this example], is ar-

bitrary. If too large, the groups will be large and few obtainable. Too small a $k$ would fail to give the advantage of systematic spacing of the quadrats in the sample sufficient opportunity of demonstrating itself."

In the present study, systematic sampling variances have been calculated with Hasel's method for all intensities and with Finney's method for all intensities except 1 in 36.

*Random sampling variances*

Since the true population figures are known, variances of random sampling can be obtained directly from them, rather than being estimated from actual random samples.

*Unrestricted random sampling.*—In sampling by this method, quadrats are distributed randomly over the entire area.

The variance of such sampling will be the total variance per quadrat for the entire area, and as such, is quite independent of the intensity of sampling. The value is obtained by dividing the sum of the squares of the deviations around the general mean over the whole stand, by the 143 degrees of freedom provided by the 144 observations.

*Stratified random sampling.*—In this type of sampling the area is subdivided into a certain number of blocks; each block then being sampled by at least two random sampling units.

A variance can be estimated for each block, and the variance of the entire population is the sum of the block variances. This variance will vary with block size and hence with sampling intensity.

In this case, the completely enumerated population permits a calculation of the block variances by means of an analysis of variance table (Snedecor 1946). The principle is to eliminate that part of the total variance (over the entire population) which is due to variations from block to block, in order to obtain the variance within the blocks (see numerical example).

For a sampling intensity of 1 in $r$, there are $N/r$ blocks of $r$ quadrats each. The intra-block variance will give the estimate of the variance of a 1 in $r$ sample, if only one sampling unit per block is taken. But in practice, two units are taken per block to obtain an estimate of the error. Thus, the intra-block variance, when there are $r$ blocks, is the estimate of a 1 in $r/2$ sample with two random sampling units per block. *Example:* an analysis of variance for the total density data gives:

| Source of variation | Degrees of freedom | Sum of squares |
|---|---|---|
| Between blocks of 36 quadrats (4 blocks) | 3 | 2068.7 |
| Within blocks of 36, between blocks of 18 | 4 | 268.5 |
| Between blocks of 18 | 7 | 2337.2 |
| Within blocks of 18, between blocks of 9 | 8 | 1782.4 |
| Between blocks of 9 | 15 | 4119.6 |
| Within blocks of 9, between blocks of 3 | 32 | 1242.6 |
| Between blocks of 3 | 47 | 5362.2 |
| Within blocks of 3, between blocks of 1 | 96 | 1978.7 |
| Total | 143 | 7340.9 |

The sums of squares are the sums of the squares of the deviations of each block sum around the mean block sum over the entire population. They are expressed in terms of unit area, i.e., the quadrat 10 by 10 meters.

For instance, for $r = 9$, the entire area is divided into 16 equal blocks of 9 unit quadrats each. The 16 block sums are:

| Block no. | Block sum | Square block sum |
|---|---|---|
| 1 | 139 | 19321 |
| 2 | 180 | 32400 |
| 3 | 180 | 32400 |
| 4 | 190 | 36100 |
| 5 | 208 | 43264 |
| 6 | 265 | 70225 |
| 7 | 115 | 13225 |
| 8 | 110 | 12100 |
| 9 | 168 | 28224 |
| 10 | 159 | 25281 |
| 11 | 77 | 5929 |
| 12 | 111 | 12321 |
| 13 | 105 | 11025 |
| 14 | 113 | 12769 |
| 15 | 132 | 17424 |
| 16 | 92 | 8464 |
| Total | 2344 | 380472 |

According to the formula (Schumacher and Chapman 1948):

$$S[(y - \bar{y})^2] = S(y^2) - \frac{[S(y)]^2}{n}$$

Each block being composed of 9 quadrats, the sum of squares expressed in terms of unit area, is $\frac{37{,}076}{9} = 4119.6$

The following illustration shows how the degrees of freedom are obtained. There are 4 blocks of 36 quadrats, thus, the number of degrees of freedom between blocks of 36 is $(n - 1)$ equals 3. Within a block of 36 there are two blocks of 18 giving $(n - 1) = 1$ degree of freedom. But there are 4 of 36, each providing one, which makes 4 degrees of freedom.

From the analysis of variance table there can then be derived:

1. The variance for unrestricted random sampling

$$s^2 = \frac{7340.9}{143} = 50.98$$

2. The estimate of the stratified random sampling variances for the following intensities

$$r = 9 \quad s^2_9 = \frac{7340.9 - 4119.6}{128} = 25.17$$

in which $7340.9$ is the total sum of squares

$$S[(y - \bar{y})^2] = 380{,}472 - \frac{(2344)^2}{16} = 37{,}076$$

$4119.6$ is the sum of squares between blocks of $9$

$128$ is the number of degrees of freedom left after subtracting $15$, degrees of freedom between blocks of $9$, from $143$, total number of degrees of freedom

$$r = 18 \quad s^2_{18} = \frac{7340.9 - 2337.2}{136} = 36.79$$

$$r = 36 \quad s^2_{36} = \frac{7340.9 - 2068.7}{140} = 37.66$$

The same computations are made for the other intensities of sampling in the same manner:

blocks of 48 - 24 - 12 - 6 - 3
48 - 16 - 8 - 4

## Results

Variances per quadrat have been calculated according to the methods described above for the following components of the stand: total density and total basal area, density and basal area of white oak (*Quercus alba* L.), hickory (*Carya* sp.), and red maple (*Acer rubrum* L.).

White oak was chosen as representative of an important species of a forest community, rather evenly distributed over the whole area; hickory as a fairly important species, with sporadic distribu-

tion; red maple as a secondary species, markedly localized.

The actual figures for the 120 by 120 m. area are as follows:

| | Density | Basal area square feet |
|---|---|---|
| Total | 2344 | 348.200 |
| White oak | 401 | 216.100 |
| Hickory | 301 | 32.850 |
| Red maple | 174 | 5.022 |

Tables I to IV give the variances *per quadrat* for systematic, unrestricted random, and stratified random sampling at different intensities of sampling.

## Interpretation

### *Comparison between Hasel's and Finney's methods of estimating the variance of systematic sampling*

Tables I to IV show that variances derived from both methods are in good

Table I. *Variance per quadrat of systematic, unrestricted, and stratified random sampling of the total population at different sampling intensities*

| Intensity of sampling (1 in r) r | Density | | | Basal area (square feet) | | |
|---|---|---|---|---|---|---|
| | Stratified random (2 plots per block) | Systematic | | Stratified random (2 plots per block) | Systematic | |
| | | Hasel's method | Finney's method | | Hasel's method | Finney's method |
| 3 | 21.78 | 14.80 | 13.08 | 1.2618 | 0.3251 | 1.8468 |
| 4 | 28.02 | 35.09 | 16.73 | 1.2752 | 0.1753 | 1.5350 |
| 6 | 28.81 | 9.39 | 23.30 | 1.2075 | 0.6748 | 1.8567 |
| 8 | 33.33 | 21.30 | 14.98 | 1.2019 | 0.1163 | 1.0310 |
| 9 | 36.79 | 14.91 | 21.43 | 1.2041 | 1.2379 | 1.3808 |
| 12 | 30.96 | 20.04 | 20.70 | 1.2078 | 1.2071 | 1.2320 |
| 16* | ..... | 26.86 | 34.67 | ..... | 1.2070 | 0.9910 |
| 18 | 37.66 | 14.51 | 25.73 | 1.2022 | 1.2297 | 1.1142 |
| 24 | 43.74 | 14.44 | 29.30 | 1.2116 | 1.1809 | 1.1060 |
| 36* | ..... | 24.71 | ..... | ..... | 1.0838 | |
| Unrestricted random (all intensities). | 50.98 | | | 1.2900 | | |

*Variances for stratified random (2 plots per block) have not been calculated at these intensities.

Table II. *Variances per quadrat of systematic, unrestricted, and stratified random sampling of white oak at different sampling intensities*

| Intensity of sampling (1 in r) r | Density | | | Basal area (square feet) | | |
|---|---|---|---|---|---|---|
| | Stratified random (2 plots per block) | Systematic | | Stratified random (2 plots per block) | Systematic | |
| | | Hasel's method | Finney's method | | Hasel's method | Finney's method |
| 3 | 3.26 | 0.47 | 4.00 | 1.4193 | 0.2264 | 1.3174 |
| 4 | 3.41 | 3.55 | 2.81 | 1.4615 | 0.8392 | 1.5560 |
| 6 | 3.38 | 2.44 | 3.69 | 1.3999 | 0.6544 | 1.5687 |
| 8 | 3.41 | 2.21 | 3.26 | 1.4269 | 0.4694 | 1.4676 |
| 9 | 3.70 | 5.17 | 3.06 | 1.3539 | 0.8160 | 0.9911 |
| 12 | 3.68 | 1.89 | 2.42 | 1.4306 | 0.8000 | 1.3771 |
| 16 | .... | 2.70 | 2.84 | ..... | 1.5127 | 1.3000 |
| 18 | 3.62 | 5.41 | 3.92 | 1.4142 | 1.1246 | 1.0996 |
| 24 | 3.75 | 3.73 | 4.45 | 1.4056 | 1.2763 | 1.2485 |
| 36 | .... | 4.83 | .... | ..... | 1.2155 | |
| Unrestricted random (all intensities). | 3.79 | | | 1.4262 | | |

TABLE III. *Variances per quadrat of systematic, unrestricted, and stratified random sampling of hickory at different sampling intensities*

| Intensity of sampling (1 in r) r | Density | | | Basal area (square feet) | | |
|---|---|---|---|---|---|---|
| | Stratified random (2 plots per block) | Systematic | | Stratified random (2 plots per block) | Systematic | |
| | | Hasel's method | Finney's method | | Hasel's method | Finney's method |
| 3 | 3.89 | 1.18 | 6.69 | 0.1124 | 0.0764 | 0.1320 |
| 4 | 3.56 | 3.86 | 3.18 | 0.1165 | 0.2280 | 0.0782 |
| 6 | 3.67 | 5.94 | 4.18 | 0.1123 | 0.0880 | 0.1107 |
| 8 | 4.24 | 3.51 | 3.30 | 0.1227 | 0.1236 | 0.1002 |
| 9 | 4.32 | 6.31 | 4.82 | 0.1237 | 0.0917 | 0.0807 |
| 12 | 4.73 | 3.89 | 4.00 | 0.1310 | 0.0838 | 0.1152 |
| 16 | .... | 3.90 | 5.11 | ..... | 0.1233 | 0.1273 |
| 18 | 4.51 | 6.69 | 4.28 | 0.1306 | 0.1197 | 0.0842 |
| 24 | 5.57 | 5.29 | 5.00 | 0.1393 | 0.1626 | 0.1336 |
| 36 | .... | 5.29 | .... | ..... | 0.1130 | |
| Unrestricted random (all intensities). | | | | | | |
| | 5.64 | | | 0.1399 | | |

TABLE IV. *Variances per quadrat of systematic, unrestricted, and stratified random sampling of red maple at different sampling intensities*

| Intensity of sampling (1 in r) r | Density | | | Basal area (square feet) | | |
|---|---|---|---|---|---|---|
| | Stratified random (2 plots per block) | Systematic | | Stratified random (2 plots per block) | Systematic | |
| | | Hasel's method | Finney's method | | Hasel's method | Finney's method |
| 3 | 4.09 | 5.40 | 5.46 | 0.006338 | 0.024185 | 0.008382 |
| 4 | 4.71 | 1.94 | 3.18 | 0.006879 | 0.002272 | 0.004653 |
| 6 | 5.34 | 4.27 | 3.24 | 0.007213 | 0.011542 | 0.006679 |
| 8 | 5.01 | 2.42 | 4.35 | 0.008070 | 0.002692 | 0.007654 |
| 9 | 4.64 | 4.92 | 5.49 | 0.007277 | 0.014543 | 0.009264 |
| 12 | 4.51 | 4.27 | 4.75 | 0.008254 | 0.008150 | 0.009678 |
| 16 | .... | 3.11 | 4.38 | ..... | 0.006309 | 0.006887 |
| 18 | 5.88 | 5.51 | 5.58 | 0.008381 | 0.010456 | 0.012162 |
| 24 | 6.50 | 5.01 | 5.46 | 0.008793 | 0.006108 | 0.004894 |
| 36 | .... | 4.98 | .... | ..... | 0.010710 | ..... |
| Unrestricted random (all intensities) | | | | | | |
| | 7.31 | | | 0.009056 | | |

agreement for high values of $r$, that is, for low intensities of sampling, but are widely discrepant at low $r$'s. Figures based on Hasel's method are either improbably low for small values of $r$, or show a very irregular pattern of variation. The estimates based on a restricted number of degrees of freedom (2, 3, 5, 7, 8 for $r$ 3, 4, 6, 8, 9) are certainly much less reliable than the figures obtained by Finney's method based on 30 to 60 degrees of freedom. However, as $r$ increases, the values obtained by the two methods converge.

In comparing random and systematic sampling, figures from Finney's method only will be used, except for the 1 in 36 sampling intensity.

### *Relationship between intensity of sampling and variance per quadrat*

*Random sampling.*—The density figures show in every case a regular increase in variance, more or less marked, as the

sampling intensity decreases. This is not so evident for the basal area where only red maple and hickory figures show that tendency, strongly for the first one, slightly for the latter. There is almost no change in variance for basal area of the total population and that of white oak.

It may be that basal area values are more regularly distributed in these instances, since a few large trees in a quadrat may have the same basal area as many small ones, although the densities will be much different.

Thus, the advantage of stratification is especially marked in sampling irregular distributions.

*Systematic sampling.*—In this case the variance per quadrat does not show much evidence of an eventual relationship with intensity.

### *Comparison between random and systematic sampling*

Estimates of variances of sample means can be derived from the estimates of variances of single observations (Tables I to IV).

If the first are expressed by the symbol $s^2_{\bar{y}}$ and the latter by $s^2_y$, $s^2_{\bar{y}}$ will be equal to $1/n s^2_y$, $n$ being the number of observations (of quadrats) in the sample taken from an infinite population.

When the population is finite, as in the present case, the estimate of the variance must be multiplied by the reducing factor $(1 - 1/r)$, since sampling errors can only affect the estimate of that fraction of the population which is not included in the sample (Schumacher and Chapman 1948).

Thus, the estimate of the variance of the sample mean will be

$$s^2_{\bar{y}} = 1/n\, s^2_y\, (1 - 1/r)$$

and its standard error

$$S.\,E. = \frac{sy\sqrt{(1 - 1/r)}}{\sqrt{n}}$$

*Efficiency of random sampling relative to systematic sampling.*—The precision of a sampling procedure has been defined as the reciprocal of its variance.

The efficiency of random $(R)$ relative to systematic sampling $(S)$ is expressed by the ratio of their respective precisions (Finney 1948)

$$Efficiency = \frac{100\ Precision\ R}{Precision\ S} = \frac{100\ Variance\ S}{Variance\ R}.$$

The variances can here be expressed per quadrat (per single observation) since each figure for the precision will introduce the same factors arising from the number of quadrats in the sample and the intensity of sampling.

Figure 3 gives the efficiencies of unrestricted and stratified random sampling relative to systematic sampling at different intensities of sampling.

For the whole series of values, the average efficiency of the stratified random sampling attains 94.4 and that of unrestricted random 80.3 (efficiency of systematic sampling = 100).

Distribution by efficiency classes for both stratified and unrestricted random is shown in the following table.

| | *Efficiency Classes* | | | | | | |
|---|---|---|---|---|---|---|---|
| | 20-39 | 40-59 | 60-79 | 80-99 | 100-119 | 120-139 | 140-159 |
| Stratified in per cent .... | 0.0 | 4.7 | 23.4 | 35.9 | 21.9 | 7.8 | 6.3 |
| Unrestricted in per cent ..... | 3.8 | 18.7 | 27.5 | 30.0 | 15.0 | 2.5 | 2.5 |

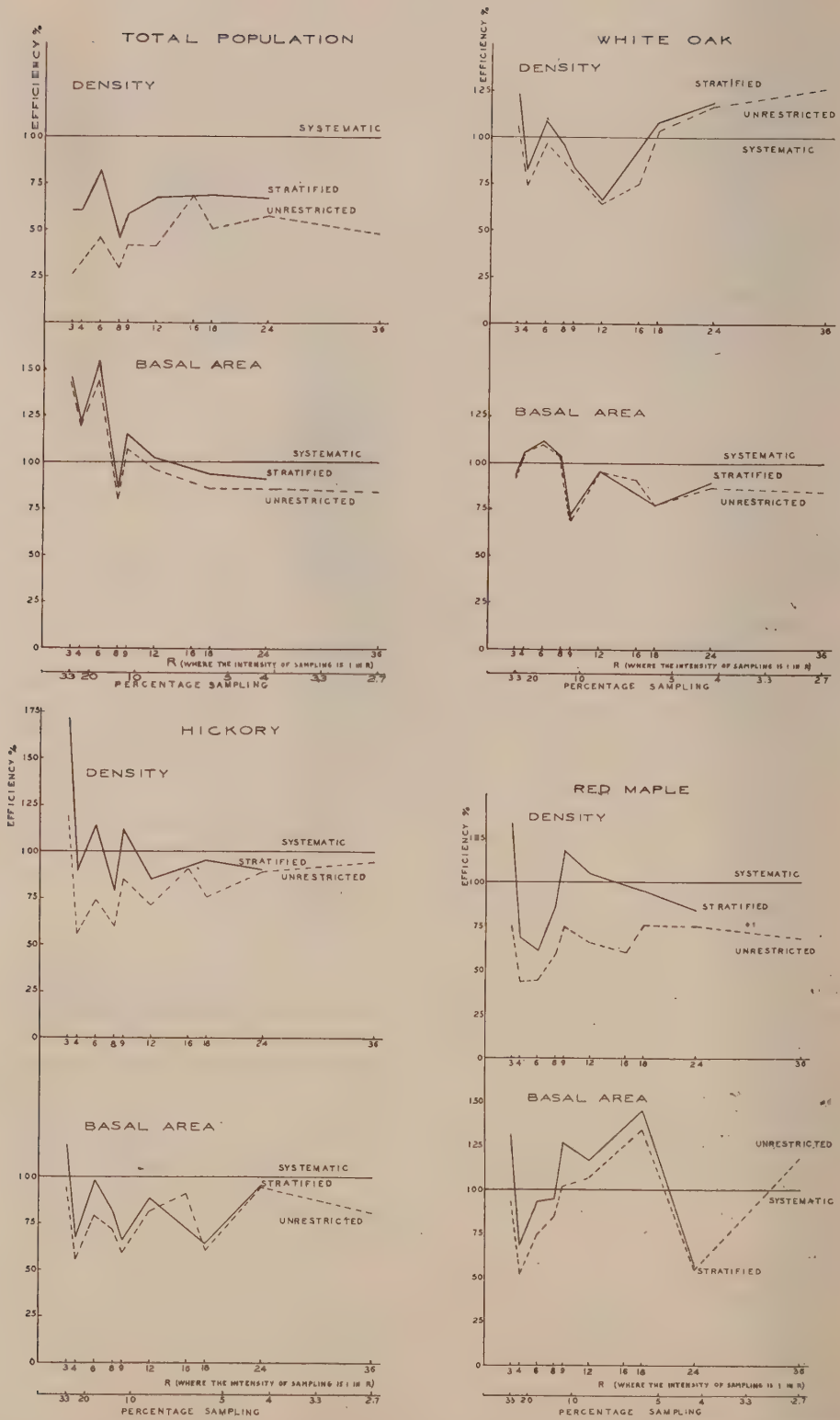


FIG. 3. Efficiency (%) of unrestricted and stratified random relative to systematic sampling at different sampling intensities

a. Total population b. White oak c. Hickory d. Red maple

Among the stratified random values, 36 per cent are more efficient than systematic sampling, 35.9 per cent are in the 80-99 class and all but 3 of them (4.7%) are above the level of 60.

The unrestricted random values are more efficient than systematic sampling in 20 per cent of the cases, and 22.5 per cent do not reach the 60 mark.

Stratification brought an average gain of 14 per cent in efficiency over unrestricted random sampling. The advantage of stratification is especially marked in sampling sporadic and irregular distributions like those of hickory and red maple, as well as densities in general (shown in the following table):

| | *Density* | | | *Basal Area* | | |
|---|---|---|---|---|---|---|
| | Stratified | Unrestricted | Gain | Stratified | Unrestricted | Gain |
| Total ..... | 63.3 | 43.9 | 19.4 | 113.4 | 102.2 | 11.2 |
| White oak ..... | 98.1 | 93.0 | 5.1 | 93.8 | 91.7 | 2.1 |
| Hickory ..... | 104.4 | 81.4 | 23.0 | 84.6 | 76.8 | 7.8 |
| Red maple .... | 93.9 | 64.0 | 29.9 | 104.0 | 89.4 | 14.6 |

*Percentage standard errors.*—The relative efficiency is a comparison between different kinds of sampling at a specified intensity but it does not indicate the intensity of sampling required in order to obtain a determined precision.

The standard error of the sample mean determines the range around the sample mean within which the chances are 2 to 1 that the true mean will fall. If expressed as a percentage of the mean it can also be readily compared with results from other data.

Percentage standard errors as given by the formula:

$$\% \text{ S. E. of sample mean} = \frac{100\, s_y \sqrt{(1-1/r)}}{\sqrt{n}\ \bar{y}}$$

are presented in graphic form (Figure 4).

Examination of these data reveals first that there is a definite correlation between magnitude of error and intensity of sampling.

Secondly, the discrepancies between sampling procedures, especially stratified random and systematic, are small compared to the size of the error itself (rarely more than 20 per cent).

Thirdly, while precisions of the estimates of large distributions are quite satisfactory at any tested intensity, errors affecting sampling of sporadic distributions of secondary importance are strikingly large even for the highest intensities. For instance, basal area estimates from a 1 in 9 sample (11.11% of the entire area) have errors of about 10 per cent for the total population, 18 per cent for white oak, 35 per cent for hickory and 62 per cent for red maple. Even with a sample size of 33.33 per cent of the entire area, the latter will still be affected by a 30 per cent error.

## Discussion and Conclusions

The object of this study was to compare random and systematic schemes of ecological sampling.

In the random sampling, each unit of the population under investigation has an equal and independent chance to be included in the sample. Only when this indispensable condition is fulfilled, is it possible to estimate a precision from data gathered in *one* sample.

Quantitative data on the composition of plant communities will be much more valuable when their accuracy is known, especially in studies dealing with the re-

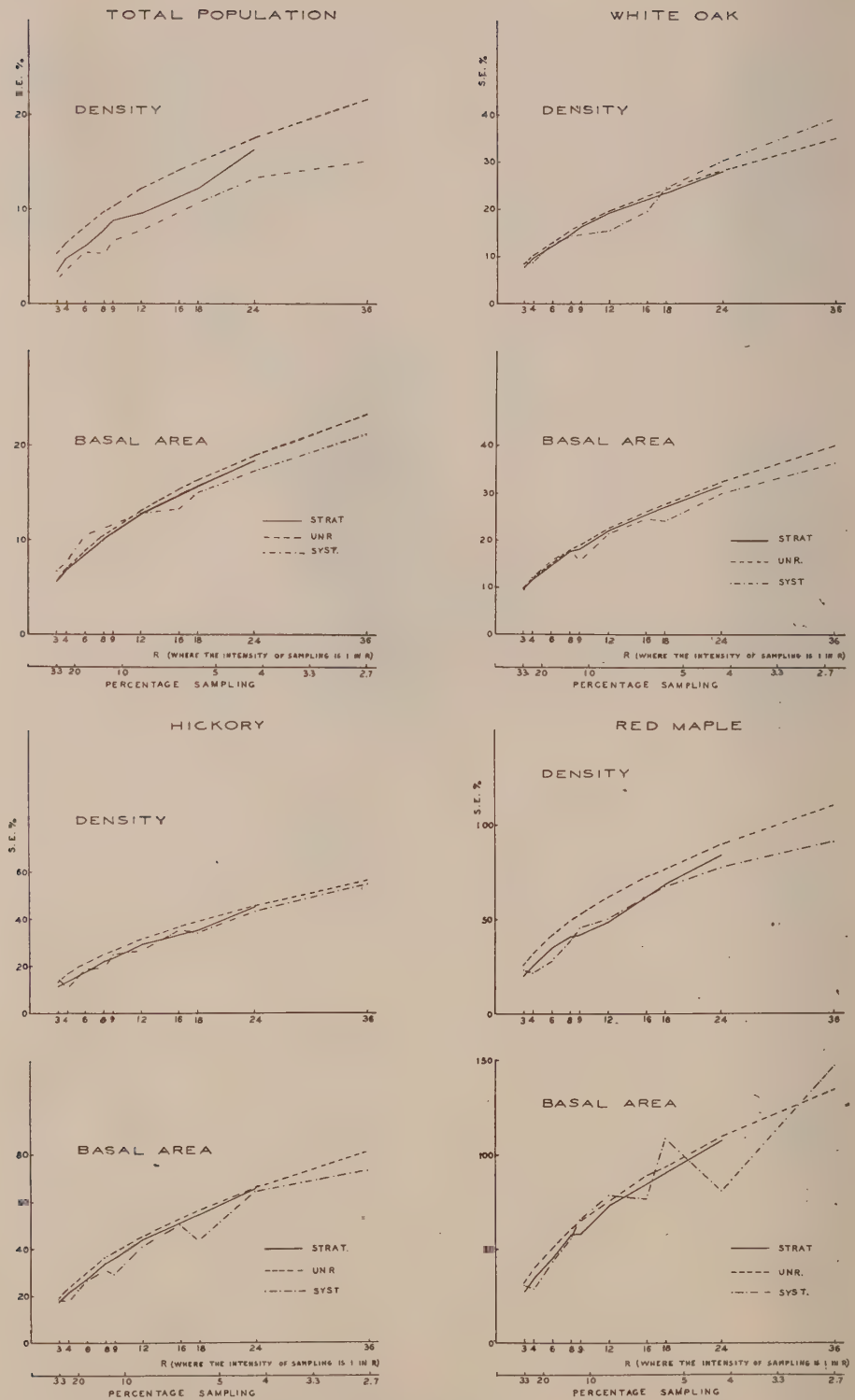


FIG. 4. Percentage standard errors of sample means at different sampling intensities
a. Total population b. White oak c. Hickory d. Red maple

lationship between environmental factors and stand composition.

The reluctance to substitute random for systematic sampling is due to the belief that the systematic sample is first much more representative, thus precise, and second more easily practicable in the field.

The data presented here show that, at least for the type of plant community to which they pertain, randomization can even produce an increase in precision, and when there is a loss, it is generally slight. This loss is much smaller, indeed, than found in similar studies on timber cruising in which Hasel (1938), for example, obtained variances twice as large for random as for systematic sampling.

The over-all average loss in efficiency, 6.6 per cent for stratified random sampling, is trifling and in only three cases did the loss exceed 40 per cent.

Stratification is always advantageous and particularly valuable in the cases of sporadic distributions. It resulted in a general gain of 14 per cent (30 per cent for red maple density).

On the viewpoint of practicability in the field, it is possible to design, without too much trouble, a scheme of stratified random sampling similar to that which is done in timber cruising ("Proportional sampling of blocks of diverse but unknown areas," Schumacher and Chapman 1948).

It thus seems sound to conclude that stratified random sampling should be widely used in ecological work since it will be almost as accurate as systematic sampling, if not more so, and it allows a reliable assessment of sampling error, for about the same amount of time involved in the field.

Incidentally, the tables of percentage standard errors give some indication of the size of error that can be expected from the sampling intensities commonly used (5 to 20 per cent of the total area). Evidently, while they yield satisfactory precisions for important components of the community, they provide only highly inaccurate estimates of secondary and scattered components.

## Summary

1. Data available from a complete enumeration of an oak-hickory forest stand have been used to compare the values of random and systematic sampling in phytosociology.
2. Variances at sampling intensities ranging from 2.8 per cent to 33.3 per cent have been computed, by Finney's method for systematic sampling, and by an analysis of variance for stratified and unrestricted random sampling. Precisions and relative efficiencies have been derived from the established variances, as well as percentage standard errors.
3. The following results were obtained:
   a. On the average, random sampling was only slightly less accurate than systematic sampling.
   b. Stratification of the random sample always yielded a gain in precision over the unrestricted form, especially in sampling sporadic distributions.
   c. Low errors of estimates were obtained only for important components of the plant community.
4. It is concluded that stratified random sampling should be used whenever reliable quantitative data are needed on stand composition. The small sacrifice in precision is indeed largely compensated for by the possibility of soundly assessing the error of sampling. Also, random sampling does not require much more field work than systematic sampling.

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# AN ALGEBRA OF POPULATION GROWTH[1]

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## Introduction

Laboratory population studies usually consist of experiments in which a small number of organisms are introduced into a suitable container. Food is added, waste products are removed, and the organisms are counted periodically. After the organisms have been counted they are replaced in the container. In general, excluding the original inoculum, organisms can enter the population only by being born in the container and can leave the experiment only by dying in the container (dead organisms usually are removed during the census).

Mathematical analysis of population growth in this kind of experiment has been attempted repeatedly (Gause 1934; Pearl 1927; Stanley 1949; Leslie 1948). These studies have been seriously hampered by the lack of a notation which is sufficiently flexible to account for the observed differences between animals, oscillatory phenomena, and physiological lag effects. An algebraic notation which seems capable of describing population growth has been developed. Some properties of two restricted applications of the notation will be described to demonstrate the kind of problems that may be examined. The possible relation of this algebra to general evolution will be stated briefly.

The notation is developed in terms of finite differences for a unisexual population. The physiological state of each individual in this population is considered to be completely defined by two measurements of the individual. It seems probable that the notation can be translated into a continuous system with two or more sexes. Also it is likely that additional measurements of the organisms can be introduced into the definition of the physiological state if necessary. It may be necessary to introduce stochastic functions in order to achieve realistic predictions.

## The Algebra

The classical Verhulst-Pearl equation of population growth does not predict the growth pattern of laboratory populations of Cladocera (Pratt 1943; Frank 1952; Slobodkin 1954 *in press*) or *Lucilia cuprina* (Nicholson 1950). This equation is conveniently written as

$$\frac{dN}{dt} = bN\left(\frac{K-N}{K}\right) \qquad (1)$$

in which $b$ is the "intrinsic rate of natural increase," that is, the maximum possible reproductive rate for the species. $N$ is the number of animals and $K$ is an environmental constant (Gause 1934).

The term $\frac{K-N}{K}$ acts to limit population increase and is usually referred to as "population density." The words "population density" or "density" will be used here in this biological sense; the concept is unrelated to the physical term, but can be thought of as a number describing the degree of crowding of the organisms of the population.

The Verhulst-Pearl equation assumes that all the organisms in the population are physiologically identical. This assumption has been experimentally denied for populations of *Daphnia obtusa* Kurz

[1] Part of this work was a portion of a doctoral dissertation presented to the faculty of Yale University in partial fulfillment of the requirements for the degree of Doctor of Philosophy, and was undertaken while the author held a Sterling Fellowship. It is a contribution from the Osborn Zoological Laboratory, Yale University, and the U. S. Fish and Wildlife Service, Sarasota, Florida.

(Slobodkin 1954 *in press*). It was also demonstrated that neither the age nor the size of a *Daphnia,* taken separately, was sufficient information to predict its physiological reactions (hence its role in population growth). The next simplest assumption is that the effect of each animal in the population on population growth is a function of its age ($j$) and its size ($i$), determined simultaneously, that is, animals of identical age and size are assumed to be physiologically identical. This does not seem too unreasonable on empirical evidence.

The variable $N$ in the Verhulst-Pearl equation is replaced by a square table, the columns of which are age categories, and the rows size categories. An entry in this table is written as $n_{i,j}$. The sum, $\sum_{i,j} n_{i,j}$ is numerically equal to $N$ in (1).

The table is written as

$$/n_{i,j}/ \qquad (2)$$

Let the relative contribution to population density of each animal in $/n_{i,j}/$ be $d_{i,j}$. That is, $d_{i,j}$ is a number expressing the relative amount of an unlimited environment occupied by an animal of age $j$ and size $i$. (In *Daphnia obtusa* populations, $/d_{i,j}/$ becomes simply a normalized table of feeding rates, since population size is limited exclusively by the available food supply.) The table, $/d_{i,j}/$, is constant, independent of density, and characteristic of the genotype.

In any given environment the population density, $D$, is computed as

$$D = F\left(\sum_{i,j}(d_{i,j}\, n_{i,j})\right) \qquad (3)$$

and is a function, $F$, of the sum of the respective products of corresponding values of $d_{i,j}$ and $n_{i,j}$. $F$ contains some constant corresponding to $K$ in (1), dependent on the actual environment of the population. $D$ varies with $\sum_{i,j}(d_{i,j}\, n_{i,j})$; expression (3) essentially replaces $\frac{K-N}{K}$ in (1).

If we consider a unisexual population, the number of individuals born of a single mother during some time interval (chosen as equal to one age interval $j$) will be a function of $D$ and of the age and size of the mother. That is,

$$b_{i,j} = f\,(D) \qquad (4)$$

where $b_{i,j}$ is the number of young born.

The total number of individuals entering the population by birth during the time interval is then

$$\sum_{i,j}\,(\,b_{i,j}\, n_{i,j}\,) = n'_{1,1} \qquad (5)$$

where $n'_{1,1}$ is the entry in the upper left hand corner of $/n_{i,j}/$ at the next time interval. It is quite likely that not all of the newborn individuals will be the same size but for the sake of simplicity the size of all newborn animals will be considered to be identical. The general properties of the notation are not affected by this simplification.

Similarly, growth and death are considered as density-dependent, so that

$$g_{i,j} = f'\,(D) \qquad (6)$$

where $g_{i,j}$ can take the values $\alpha$, $\beta$, and $\gamma$ only.

Biologically, $\alpha$ is equivalent to death, $\beta$ is equivalent to survival with no size increase, and $\gamma$ to survival with size increase.

We assume an age scale such that it is impossible for any organism to increase more than one size category from one time interval to the next.

The mathematical properties of $f'\,(D)$ are completely defined by the multiplication table

| | $\alpha$ | $\beta$ | $\gamma$ |
|---|---|---|---|
| $\alpha$ | 1 | 0 | 0 |
| $\beta$ | 0 | 1 | 0 |
| $\gamma$ | 0 | 0 | 1 |

(7)

An operator $T$ can now be defined, which acts to move $/n_{i,j}/$ from one time interval to the next, by making the following substitutions:

*for $n_{1,1}$ substitute $n'_{1,1}$ as defined by (5);* (8)[2]

*for $n_{i>1,j>1}$ substitute*

$$(\beta g_{i,j-1} n_{i,j-1} + \gamma g_{i-1,j-1} n_{i-1,j-1}) \quad (9)$$

By (7), any product of $g_{i,j}$'s reduces to *1* or *0*, so that (9) becomes $n'_{i,j}$.

We can therefore write

$$T/n_{i,j}/ = /n'_{i,j}/ \quad (10)$$

$D'$, the population density value for $/n'_{i,j}/$, is now re-evaluated by (3); and (4), (5), (6), (8), and (9) are successively applied to produce

$$T^2/n_{i,j}/$$

Population $/n_{i,j}/$, $k$ time intervals later, can be written as

$$T^k/n_{i,j}/ \quad (11)$$

Since it is of interest to speak of the complete history of a population, we introduce the notation $T^*/n_{i,j}/$, where

$$T^*/n_{i,j}/ \equiv T^k/n_{i,j}/ \text{ for all } k. \quad (11a)$$

Any empirical assumptions that may seem of interest can be made about density, birth, growth, and death without making the notation inapplicable.

## A Restricted Equilibrium Population

Consider an equilibrium population $Te^*/n_{i,j}/$.

A. Let $f(D)$ and $f'(D)$ be completely deterministic, so that all the animals in a particular age-size category act as a unit.

B. Let $f(D)$ take only integers as values in order to exclude fractional birth rates.

C. Let $f'(D)=\alpha$ only at $t$, where there are $t$ age categories and $t$ size categories in $Te^*/n_{i,j}/$, so that no animals leave the table except at its end.

D. Let $D$ and $\sum_{i,j} n_{i,j}$ be constant for all values of $k$.

(D) defines $Te^*/n_{i,j}/$ as an equilibrium population in the narrowest biological sense of the term. (A), (B), and (C) are simplifying assumptions.

The following statements about $Te^*/n_{i,j}/$ will then be valid. Formal proofs will not be given here.

$$\sum_{i,j} (\alpha g_{i,j} n_{i,j}) = n'_{1,1} \quad (12)$$

That is, (D) requires that the number of animals entering the population by birth equal the number leaving by death.

$$\text{For all } j, \ \sum_i n_{i,j} \text{ is constant.} \quad (13)$$

The number of animals in any age category is equal to the number in any other age category.

*For each $j$ there exists one and only one non-empty size category, $i$, and this value of $i$ is the same for all $k$.* (14)

In effect, this states that all the individuals in the population have an identical growth rate. The proof involves induction. We know by (5) that for $j=1$, $i=1$. For $j=2$, the value of $i$ depends on $f'(D)$, but this value will be the same for all $k$ by assumption (D). The growth rate of all animals $n_{i,2}$ will therefore be the same. Assuming the result for all animals $n_{i,q}$, assumption (D) gives the result for all animals $n_{i,q+1}$, completing the proof.

*There exists one and only one $j \leq t$, i.e. $h$, for which $b_{i,h}=1$. For all $j \neq h$, $b_{i,j}=0$.* (15)

That is, each animal must reproduce itself once, and only once, before it dies and since all animals have identical growth rates by (14), and since age and size define the physiological condition of the animal, each animal will reproduce at the same age. Birth of more than one animal from a single parent will deny (12) and (13).

[2] In the case where all newborn animals are not of the same size replace (8) by (8′). That is:

*for $n_{1,1}; n_{2,1}; n_{s,1}$ substitute $n'_{1,1}; n'_{2,1}; n'_{m,1}$ where $(s, m < t)$ and $n'_{1,1}; n'_{2,1}; n'_{m,1}$ is the size frequency distribution of newborn animals.* (8′)

A similar sort of modification can be introduced if the size of the newborn animal is constant for the offspring of animals of each age-size category of parents, but differs between age-size categories of parents, or if the size frequency distribution of newborn animals depends on the age and size of the parents.

Considering $f(D)$ to be linear with $D$, equilibrium populations of the sort $Te^*/n_{i,j}/$ can only occur among species in which there exists a maximum in the three-dimensional curve of birth rate plotted against age and size.

## A Restricted Oscillatory Population

Consider a population $Tos^*/n_{i,j}/$.

Let $Tos^e/n_{i,j}/$ be defined as $Tos^*/n_{i,j}/$ at all time intervals for which $k$ (as defined in (11)) is even.

$Tos^e/n_{i,j}/ \equiv Tos^*/n_{i,j}/$ *for all* $k$ *even.* (16)

Similarly, let $Tos^o/n_{i,j}/$ be defined as $Tos^*/n_{i,j}/$ at all time intervals for which $k$ is odd. (16a)

E. Let the restrictions (A), (B), and (C) apply to $Tos^*/n_{i,j}/$.

F. Let $\sum_i n_{i,j}=0$ for all even values of $j$, and let $\sum_i n_{i,j}=x$ for all odd values of $j$ in $Tos^e/n_{i,j}/$.

G. Let $\sum_i n_{i,j}=x$ for all even values of $j$ and let $\sum_i n_{i,j}=0$ for all odd values of $j$ in $Tos^o/n_{i,j}/$.

We define:

$$D^e=F\left(\sum_{i,j}(d_{i,j}\,n_{i,j})\right) \text{ of } Tos^e/n_{i,j}/ \quad (17)$$

$$D^o=F\left(\sum_{i,j}(d_{i,j}\,n_{i,j})\right) \text{ of } Tos^o/n_{i,j}/$$

H. Let $D^o$ and $D^e$ be constant.

I. Let

$f(D^o)=1$ for a unique even value of $j$.

$f(D^e)=0$ for all values of $j$.

Population $Tos^*/n_{i,j}/$ will oscillate in population density and age structure with a period of $2k$, and may or may not oscillate in numbers.

If $t$ is odd, the amplitude of the oscillation in $\sum_{i,j} n_{i,j}$ will be $x$.

If $t$ is even, there will be no oscillation in $\sum_{i,j} n_{i,j}$.

More generally,

$$\left(x=\sum_i n_{i,1}=\sum_i n_{i,t}\right) \text{ in } Tos^*/n_{i,j}/ \text{ implies} \quad (18)$$

*that* $\sum_{i,j} n_{i,j}$ *will oscillate with an amplitude* $x$.

$$\sum_i n_{i,1} \neq \sum_i n_{i,t} \text{ in } Tos^*/n_{i,j}/ \text{ implies that}$$

$$\sum_{i,j} n_{i,j}=xt \text{ and is constant for all } k. \quad (18a)$$

This gives the result that whether or not $Tos^*/n_{i,j}/$ will oscillate in numbers depends on the life expectancy of the individual animals. For one set of life expectancies, the population will be stable, while, for another set, the population will oscillate.

Population $Tos^*/n_{i,j}/$ does not seem too dissimilar from actual populations of *Daphnia*. *Daphnia obtusa* populations maintain a remarkably stable population equilibrium at 20° C. If the temperature is lowered to 14° C., small continual oscillations are produced (Slobodkin 1954 *in press*). In *Daphnia magna* populations, relative stability occurs at 18° C., while large oscillations occur at 25° C. (Pratt 1943). Temperature change may be expected to change the life expectancy of *Daphnia* (Pratt 1943; MacArthur and Baillie 1929). The model $Tos^*/n_{i,j}/$ therefore predicts in a general way the observed relation between oscillation and temperature in *Daphnia magna* and *Daphnia obtusa*.

If $f(D)$ is linear with $D$, $Tos^*/n_{i,j}/$ differs from $Te^*/n_{i,j}/$ in the required relation between birth rate and age. For $Tos^*/n_{i,j}/$ it is sufficient to require a plateau not wider than $2j$ in the birth curve, while for $Te^*/n_{i,j}/$ it is necessary that the curve of birth rate against age show a unique maximum.

## Application to an Evolutionary Problem

$f(D)$ or $f'(D)$ can be chosen so as to cause the population to oscillate to extinction. In particular, the chance of oscillating to extinction is increased as the amplitude of the dependence of the birth rate on density is decreased.

In nature, most species can be considered as occupying a set of spatial regions, each one of which will contain a separate population. These populations

can be treated as independent units, except that occasionally an individual or group of individuals from one region will migrate (or be carried by accident) to another region.

Let us consider that a species $S$ exists which is completely homozygous except for a gene determining reproductive rate. This occurs in a pair of alleles, $r_o$ and $r_e$. The genotype $r_o$ is such that a population $Sr_o$ composed exclusively of $r_o$ individuals, will have a high, density-independent reproductive rate and will therefore oscillate. The genotype $r_e$ is such that a population, $Sr_e$, composed exclusively of $r_e$ individuals, will have a density-dependent birth rate lower than that of population $Sr_o$ and will not oscillate. The effect of natural selection on the relative frequencies of $r_o$ and $r_e$ will then depend on the migration rate between the regions occupied by $S$, and the probability as a function of time, that $Sr_o$ will oscillate to extinction.

Let species $S$ consist of a set of separate populations $Sr_o$ and $Sr_e$. In the absence of migration, each population $Sr_o$ will become extinct, while each population $Sr_e$ will persist indefinitely.

Let $t_o$ be the time interval such that there is a probability, $P_o$, that any $Sr_o$ will become extinct during that time interval, in the absence of migration.

Let $t_m$ be the time interval such that the probability of a migrant arriving at a particular region is $P_o$. That is, the migration rate varies as $t_m^{-1}$.

If $t_m >> t_o$, the genotype $r_e$ will have a selective advantage over $r_o$. This follows, since each $Sr_o$ will probably be extinct before migration can occur from, or to, the region which it occupies.

As $t_m^{-1}$ increases, the selective advantage will shift in favor of $r_o$. As the rate of migration increases, more populations will consist of mixtures of $r_o$ and $r_e$ individuals, and according to classical population genetics, whenever $r_o$ and $r_e$ individuals occur in the same population, $r_o$ will have a selective advantage in that population.

Increase of the rate of migration is equivalent to increasing the life expectancy of each $Sr_o$, since the chance of an $Sr_o$ being saved from extinction by the arrival of migrants increases. If $r_e$ is actually eliminated from all populations, then $S$ can continue to survive only by relatively rapid migration of individuals from region to region, so that the population is increasing in one region, while it is decreasing in others.

If the migratory rate becomes too rapid and random, all of the species $S$ essentially becomes one population, $Sr_o$, which will eventually oscillate to extinction.

If the migratory rate between regions is lowered by some external mechanism, such as climatic change, after $r_e$ has been eliminated from $S$, then species $S$ will become either extinct or very rare.

We would expect that most species with a physiological reproductive rate which is relatively independent of density will have developed either a method for increasing the number of migrants during critical periods of population oscillation or a secondary behavioral method of making the reproductive rate density-dependent.

Both insects and vertebrates have fairly constant birth rates which would be expected to produce population oscillations. Three general methods of insuring population survival occur in these groups.

In the holometabolous insects, exclusive of the Hymenoptera, it is possible to consider the production of winged adults as a device for increasing the rate of migration between regions. A particularly interesting case, from this viewpoint, is the relation between food supply and metamorphosis in the dipteran, *Oligarces paradoxus*. Ulrich (1940) has shown that this species is normally parthenogenetic and paedogenetic, with a variable birth rate dependent on the food supply. As the food supply deteriorates in quality or quantity, the reproductive rate de-

creases and the young born in these reduced broods metamorphose into winged adults which then leave the region occupied by the parent larvae. In these Diptera, the function of winged adults as a migratory mechanism is obvious.

If the adult holometabolous insects are primarily methods of increasing the rate of migration, it would be expected that adults of any holometabolous species would not be seriously limited by competition with other adults of the same species and this seems true in general.

Analysis of the hypothetical species *S* indicates that migration distributed at random, in time, will not be as effective in insuring the survival of the species as will migration occurring at critical points of the population history. The highly seasonal cycle of holometabolous insects seems of interest in this connection.

Among the non-social insects, the young generally do not inhabit the same environment as the adults. In the case of *Lucilia cuprina* (Nicholson 1950), if the young and adults should be maintained in a situation in which contact with their own young is unavoidable, extreme population oscillations occur, while in the case of grain insects maintained in flour, eggs and pupae are eaten by the adults and in some cases by the larvae (Crombie 1947; Park and Frank 1950). Eating of immature stages acts to introduce secondary density-dependence into the birth rate.

In fish with planktonic larvae, the relation between young and adults is similar to that in insects. That is, normally the young and adults occupy two separate environments; eating of young by adults is a common occurrence only when the two are in contact.

In the Hymenoptera, birds, and mammals a new form of behavioral density-dependence is introduced, parental care of the young. Here the density-dependence is mediated through the effect of density on the adults. It is possible that excess population density will make rearing of young animals exceedingly difficult and will effectively lower the reproductive rate.

The general conclusion that can be made from our analysis of species *S* is that a low, density-dependent birth rate can only evolve under special conditions of animal distribution. At the same time, a high constant birth rate may lead to species extinction. Secondary density-dependence, mediated through behavioral mechanisms or mechanisms for increasing the migratory rate, will then have a selective advantage, after the species has developed a constant birth rate.

These conclusions seem at least partially verified by the available information.

## Acknowledgments

Professor G. Evelyn Hutchinson provided invaluable encouragement and advice during the course of this work. David Calhoun of Yale University and William Malkus of the Woods Hole Oceanographic Institution helped in the mathematical formulation.

## Conclusion

The algebra $T/n_{i,j}/$ seems to offer a technique for the analysis of a fairly wide range of population problems, permitting ecological and evolutionary consequences to be deduced from physiological assumptions. In the cases examined, the conclusions inferred by use of $T/n_{i,j}/$ seem to agree fairly well with available data.

## Summary

1. A notation has been developed which is sufficiently general to describe the growth of populations of animals.

2. Two models of populations have been described, one of which has been found to have properties similar to those of *Daphnia* populations; in particular, whether or not $Tos^*/n_{i,j}/$ will oscillate in total number of animals depends on the life expectancy of the individual animals.

3. A hypothetical species, *S*, has been constructed based on the general prop-

erties of $T/n_{i,j}/$, and it has been shown that a situation could exist in which a genotype with a low reproductive rate would have a selective advantage over a genotype with a high reproductive rate Some inferences of $S$ for general evolutionary theory are mentioned and relevant cases are cited.

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# EFFECTS OF PRESCRIBED BURNING ON GROUND COVER IN THE NEW JERSEY PINE REGION

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At least since the late 19th century foresters have been searching for an economically feasible method of returning the present forests of the New Jersey pine region to levels of higher production (Vermeule, Pinchot, Hollick, Smith, and Gifford 1900). Slow but continuous progress has been made since that time in fire control, public education, and the acquisition of knowledge of the silvicultural relationships of the forest trees. Now after nearly 15 years of experimentation by state and federal investigators, the application of prescribed burning has been suggested as a silvicultural practice for improving the upland forests of the region.

As a result of its success in experimental areas, the practice shows promise of becoming wide-spread in the near future. Hence, it becomes more important that we understand as many as possible of the effects that will be created by the increased use of the practice. The foresters have and will continue to accumulate data on estimated timber yields and per acre costs of the management practice. Various other interested groups in and around the area are cooperating with the foresters in initiating studies of the broader aspects of the practice.

At present there are several questions that warrant careful investigation. First, will the change in vegetation resulting from the practice make any significant alteration in the hydrologic relationships of the region? This study is already past the planning stage. Second, how will the management practice influence the wildlife in this very important game-producing area of the state? Third, how will the practice influence the productive potential of the forest soils of the region? Fourth, how will the practice influence agricultural industries, now flourishing in the region, through altering helpful and harmful insect populations and by increasing or decreasing the abundance of native plant species that harbor pathogens of cultivated species? These are some of the questions which should be investigated while such a management plan as prescribed burning is in the early stages of application.

Several cooperating workers have already published on the methods used and the effectiveness of this practice in favoring the more valuable pine over the less valuable oak species (Little 1946, Little, Allen, and Somes 1948, Little, Allen, and Moore 1948, Somes and Moorhead 1950). For the most part, these studies have been focused on the arborescent species, data having been obtained on (1) growth, survival, and damage to individuals already present and (2) the effect of altered conditions on the reproduction of the various species. The present study is concerned with the influence of this management practice on the shrub, herb, and moss layers of the plant community.

Prescribed burning is based on the principle that fire judiciously used favors a fire subclimax forest of high pine composition. Data obtained by the authors cited above indicate that these pine stands

will be far more productive than those in which occasional destructive uncontrolled fires occur or in which fires are entirely excluded. Prescribed burning improves the seed bed for pine, produces a much poorer seed bed for oak, and greatly reduces the danger of destructive wild fires. The pines of this region require a mineral seed bed or at least one with a very shallow organic layer (Little and Moore 1949). A deep litter layer, a natural characteristic of much of the pine region, discourages prolific pine reproduction but makes an excellent seed bed for the oaks. Prescribed burning prevents the accumulation of large quantities of litter and dead brush. Thus, in addition to seed bed preparation, the fuel for wild fires is so reduced that such fires are both less damaging and more easily suppressed than in areas not so managed.

Prescribed burning is done in the winter under conditions favorable for low fire intensity, and preferably when the temperature of the tree trunks is low so that injury will be at a minimum. The burning is carried out under the supervision of trained personnel, and is limited to areas where crop trees are large enough (more than 2 in. d.b.h. on upland sites) so that damage is not important. Intervals between burns are not automatic, but depend on fuel accumulation, need for fuel reduction, etc. However, the average interval once burning has started may be 4 or 5 years.

The present study was made in one block of experimental plots for prescribed burning located in Lebanon State Forest, New Jersey. More specifically, the plots are located in the area adjacent to North Branch Road and between Mount Misery Road and the small stream called Middle Branch; the geographic coordinates are approximately N 39° 54.5′ and W 74° 30′. The establishment, treatment, and maintenance of these plots have been a cooperative undertaking of the New Jersey Department of Conservation and Economic Development and the Northeastern Forest Experiment Station of the U. S. Forest Service.

The existing forest in the area where the experimental plots were established is similar to the oak stand described in a recent paper by Buell and Cantlon (1950). The oaks predominate in the canopy although there is a liberal scattering of pines. The pines are not reproducing. There is a very well-developed shrub layer in which heaths predominate, but both herbs and bryophytes are sparse. On the ground there is a large accumulation of litter. Since the oaks are poor in quality and low in value, the objective of the foresters is to convert the forest to one of pine dominance with maximum yield of pine timber.

The plots are on coarse sandy soils low in clay fractions and having a pronounced podzol profile. They have been mapped mostly as Sassafras sand, but include also some Lakewood sandy loam (deep phase) (Lee 1923). As a result of the coarseness of the soil and gentleness of the slopes, surface runoff and consequently erosion are practically non-existent in this region so long as there is some vegetation on the area. Unlike other sections with finer soils or steeper slopes, areas in the pine region do not need a dense cover of vegetation, or vegetation and litter covers, to check erosion.

The mean annual precipitation in the region is about 45 inches, evenly distributed throughout the year. The crop growing season is about 178 days. The average January temperature is about 32° F, the July, 75° F (Reichelderfer, *et al.* 1941).

This study was made possible through grants by the American Cranberry Grower's Association and the Rutgers University Research Council and through the aid and cooperation of the U. S. Forest Service personnel at New Lisbon, New Jersey. The authors wish to express their appreciation to all three groups. The authors are indebted to Dr.

Silas Little for his critical reading of the manuscript.

## Methods

The 16 five-acre plots (5 × 10 chains) on which the studies were made were established in 1936. These plots were subdivided for sampling by the Forest Service as outlined in Figure 1. Eight different treatments were initiated in 1937. Two of them were left as controls, two were burned annually, and two each were burned every two, three, four, five, ten, and fifteen years respectively. The burning was done in the winters as described by Little and Moore (1945) and by Somes and Moorhead (1950). On half of each five-acre plot the burning treatments ceased after the winter of 1945-46, and the following winter the oak overstory was cut, an operation necessary to get optimum establishment and growth of young pines. On the other half of each plot the burning treatments have continued and there had been no cutting at the time of the present study. Thus, since each of the above eight treatments have both a cut and an uncut half, there are actually 16 different treatment combinations. There are two replicates of each of these.

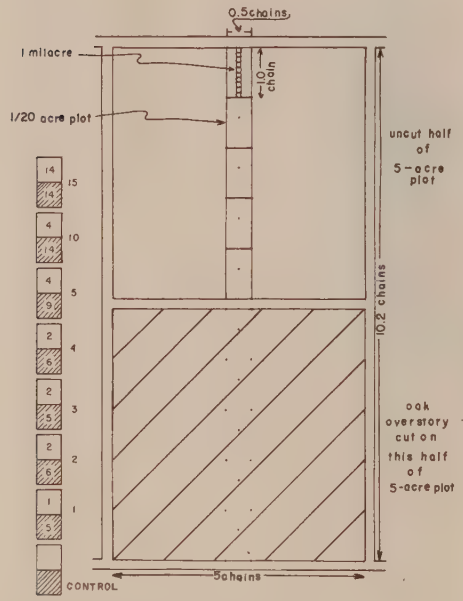


Fig. 1. Diagram of plot lay-out. One chain is equal to approximately 20 meters and a milacre quadrat is about 2 meters square. Plot diagrams at left show number of growing seasons elapsed between last burn and the time of the study. Numbers at right indicate interval in years between burns. Numbers in plots, years since last burn. Shaded half, cut in winter of 1946-47.

The data for the present study were obtained in the summer of 1950. Part of the sampling was done on milacre quadrats (approximately 2 × 2 meters), a total of ten being studied for each treatment combination. There were five such quadrats on each of the two replicates. In these quadrats tree seedling counts and an estimate of cover for the shrub, herb, and moss (including lichens) layers were made.

To supplement these data, a study of cover was made on some of the treatments using the line intercept method (Buell and Cantlon 1950). Data were obtained from the uncut halves of the controls and the plots burned annually and every 3, 5, and 15 years as well as from the cut halves of the controls and the plots burned annually and every three years. Both replicates of each of those treatments were studied. Sampling by this method was done along two lines, one on each side of the 0.5 × 5.0 chain strip established in each half-plot by the Forest Service (Figure 1). Cover and open space in the tree, shrub and herb layers were estimated over a total of 400 meters of linear distance in each treatment. One-half of this sample was obtained from each of the two replicates.

All species encountered in the quadrats were collected for identification and are on file in the Chrysler Herbarium of Rutgers University. Nomenclature for the vascular species follows that of Fernald (1950). None of the non-vascular species was collected or identified.

## Results

In interpreting the results of sampling on the plots of different burn frequency, it is important to keep in mind the length of time elapsed since each of the plots was last burned. All but the control plots were treated by prescribed burning in 1937. Thus, in the uncut portions at the time of sampling it was the fourteenth growing season since the 15-year plots had been burned, the fourth growing season for the 10- and 5-year plots, the second growing season for the 4-, 3-, and 2-year plots, and the first season for the 1-year plots. The cut portions were not burned after the winter of 1945-46. Therefore, the summer of 1950, the time of sampling was the following number of years since burning (and cutting): 14(4), 14(4), 9(4), 6(4), 5(4), 6(4), and 5(4) (See diagram left side of Fig. 1). The fact there are differences in the vegetation in plots having different burning frequencies, even though the length of elapsed time since the last burn is in some cases the same, seems to demonstrate the importance of the total burning regime.

The data indicate that the frequency of prescribed burning has a marked effect on the lower vegetation layers. With increased frequency of burning there is a rather sharp reduction in the litter (Fig. 2A, curve L). The shrub layer is also greatly reduced as shown by in-

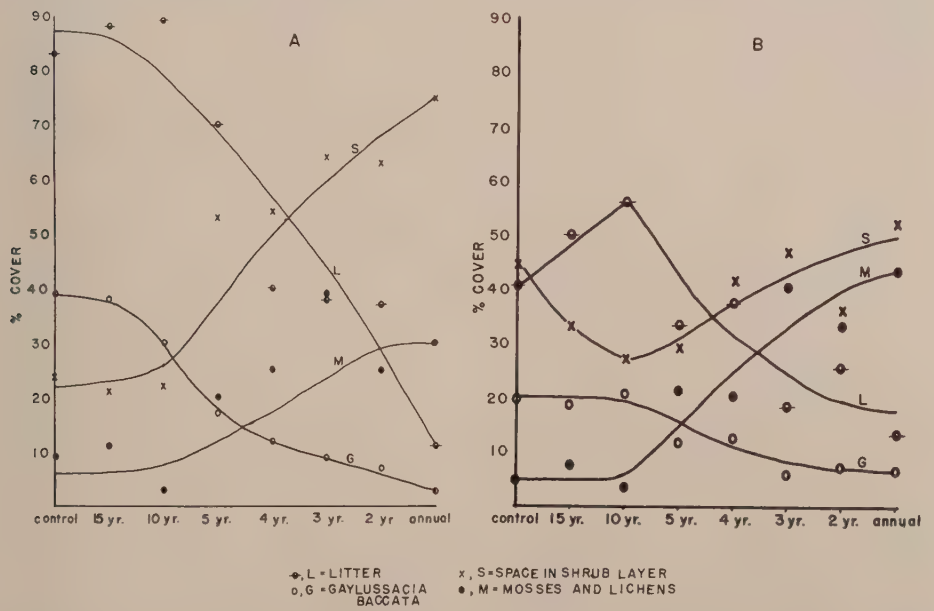


Fig. 2. A. Curves based on data from milacre quadrats in uncut portion of plots. B. Curves based on data from milacre quadrats in cut portions of plots. Legend same for both A. and B. Per cent cover refers to area covered.

crease in the unoccupied space in this layer (Fig. 2A, S). There is not, however, a uniform reduction in all species. Cover of *Gaylussacia baccata* was approximately 40% in the controls and only about 3% in the plots burned annually (Fig. 2A, curve G). Cover of *Gaylussacia frondosa* was 14% in the controls and only 0.5% in the annually burned plots. *Vaccinium vacillans* showed no regular trend in cover change until burns became more frequent than every three years. In the plots burned annually, the cover of this species is approximately one-

half of that in the less frequently burned plots.

In Figure 3, the cover data obtained by the line intercept method for three shrub species are presented as the per cent of total shrub cover. Although all

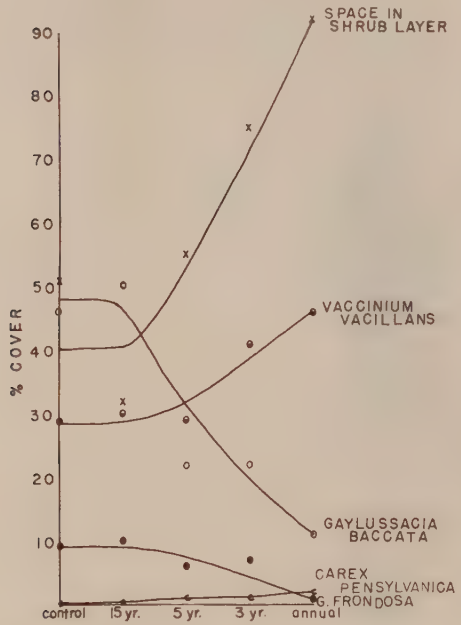


FIG. 3. Curves based on data obtained from line intercept method in uncut portions of plots as indicated. Per cent cover for the three shrub species refers to per cent each contributes to the total cover. Space refers to total area in the shrub layer unoccupied. *Carex pensylvanica* is plotted as estimated per cent of area covered.

shrub species have lower actual cover values in the most frequently burned plots, these curves indicate that in contribution to the cover *Gaylussacia baccata* and *G. frondosa* become less important and *Vaccinium vacillans* becomes relatively more important. Open space in the shrub layer is again shown to increase greatly with more frequent burning.

There were 17 additional shrub species encountered in the sampling. Of these, the shrub oaks, *Quercus ilicifolia* and *Q. prinoides* become more important in the shrub layer with increasing burn frequency. *Gaultheria procumbens,* on the other hand, becomes less important. Due to the widely scattered distribution of the other shrub species, no definite relationship to burning frequency could be ascertained from the present sampling. These include *Smilax glauca, Pieris mariana, Comptonia peregrina, Kalmia angustifolia, Crataegus uniflora, Ilex glabra, Amelanchier arborea, Aronia melanocarpa , Rhus copallina, Vitis aestivalis, Epigaea repens, Vaccinium angustifolium,* and *Kalmia latifolia.*

In general, the herbaceous layer increases in cover with increasing frequency of burning. The total cover of angiospermous herbs was only 0.3 per cent in the controls while in the annually burned plots it was 5.5 per cent. Much of this increase in cover is contributed by *Carex pensylvanica* (Figure 3) and *Andropogon scoparius.* Lemon (1949) has shown that survival and increase of herbs under prescribed burning are related to life-form and life history of the species concerned.

The bracken fern, *Pteridium aquilinum,* is the only herb which the sampling indicated to have higher cover values in the less frequently burned plots. However, the apparent reduction in response to burning is not real. This species is quite spotty in occurrence in upland forest stands of the region and upon checking the 1936-37 survey of the plots, it was found that at that time the heaviest cover of bracken happened to be on the plots which since have had the least burning. Unfortunately, the 1936-37 survey was made in the winter and by several different workers. It was useful, therefore, only for checking and could not be used for exact comparison of cover values. Little has written, in correspondence with the authors, that in specific stands, the bracken fern actually increased with frequent burning.

Cover by the moss and lichen layer increases with burning frequency (Figure 2A). In sampling, all species in this

layer were considered together and from these data it is not possible to determine which of the species contribute most to the apparent increase in cover in the more frequently burned plots.

Cutting of the oak overstory and cessation of burning for four years do not entirely obscure the effects of previous differences in burn frequency. These two factors, however, do result in decreased differences between the plots (Figure 2B). Cover of the litter layer and of *Gaylussacia baccata* still are less in the most frequently burned plots, while cover by the moss and lichen layers has increased considerably. These trends are similar to those shown in the uncut portions.

Little difference was found in the amount of open space in the shrub layer between the cut portions of the controls and of the annually burned plots. In the cut portions, the smallest amount of open space in the shrub layer occurred in the less frequently burned plots.

In an attempt to determine the effects of cutting upon the understory vegetation, the data from the cut and the uncut portions of all plots, regardless of burning treatment, were totaled separately. From these totals, average cover was then calculated for each condition (cut and uncut) for several species and the layers of vegetation concerned (Figure 4). It should be pointed out that since burning also ceased at the time the overstory was cut, the differences are in part due to the cessation of burning.

Herb cover, shrub cover, and cover of *Vaccinium vacillans, Pinus* spp., the arborescent oaks, *Quercus ilicifolia,* and *Carex pensylvanica* are all greater in the cut portions (Fig. 4). Litter cover and cover of *Gaylussacia baccata* are less. All of these apparent responses to cutting might well have been anticipated except the decreased cover of *Gaylussacia baccata.* This apparent decrease was further supported by checking against the original records for the plots and by observations of areas of dead and dying stems of this species in the cut portions of many plots. The actual cause of death is unknown.

Some of the greatest differences in the lower vegetation layers were found between the cut and uncut portions of the annually burned plots. Data from the line intercept study show that total ground cover in the annually burned plots averages around 10 per cent in the uncut portions and approximately 50 per cent where the study was made in the fourth growing season since cutting (fifth since burning). Much of this increase in ground cover is contributed by arborescent species through growth of sapling pines and oak stump sprouts. Thus, the actual ground cover contributed by arborescent oaks is 2 per cent in the uncut portions and 16 per cent in the cut portions. For the pines, the cover is approximately 1 per cent and 9 per cent respectively.

Apparently some of the true shrubs also contribute to this increase in ground cover following cutting and cessation of burning on these plots previously burned annually. Cover of *Vaccinium vacillans* was found to be approximately 9 per cent in the uncut portions and 20 per cent in the cut portions of these plots. Cover of *Gaylussacia baccata* was only 2 per cent and 4 per cent respectively. The shrub oaks, *Quercus ilicifolia* and *Q. prinoides,* were found to have a slightly lower cover in the cut plots but the difference is probably not significant considering the spotty distribution of these two species.

Considerable change also occurs in the herb and moss layers where these frequently burned plots are cut and released from burning. Total herb cover was found to be 2 per cent in the uncut and 16 per cent in the cut portions. By far the greatest part of this cover is contributed by *Carex pensylvanica* and *Andropogon scoparius.* The milacre quadrat data indicate that the average cover by mosses and lichens was 30 per cent

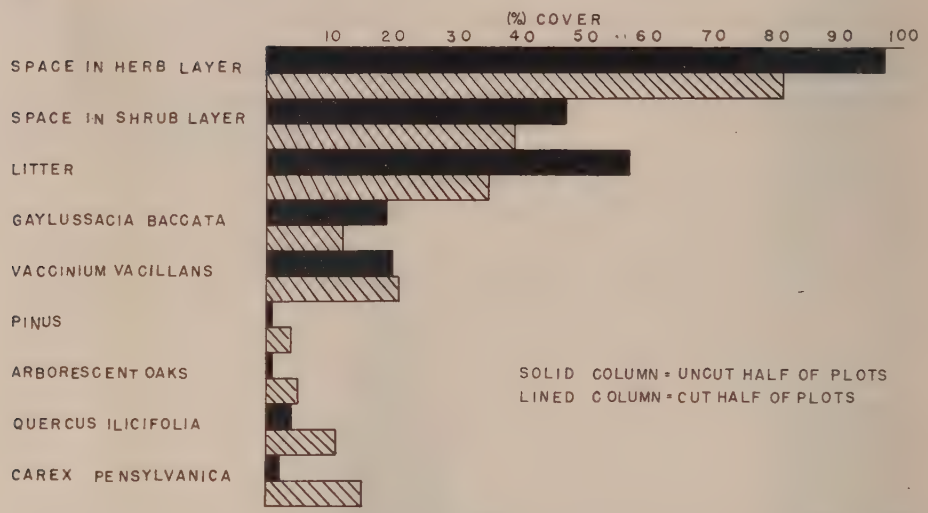


FIG. 4. Comparison of cover estimates made in milacre quadrats in cut and uncut half of plots. This is based on averages for all plots. Space refers to that portion of the area unoccupied in the layer concerned.

in the uncut and 44 per cent in the cut portions. Much of this higher cover is due to a greater abundance of lichens in the cut portions. The forest floor in the uncut portions has a green mossy look; these areas are more gray-green from lichens in the cut portions.

## DISCUSSION

In the forests of the New Jersey pine region prescribed burning has been shown to have a marked effect upon the lower vegetation layers. An evaluation of these effects is, of course, difficult at this early stage of the study. Without doubt, the success of the practice as a silvicultural technique is due to its alteration of these lower layers. As to the effects of these changes in vegetation on some of the other natural ecological relationships of the region, less of a positive nature can be stated.

The marked reduction in the litter layer is brought about when burning becomes more frequent than every five years (Figure 2, part A). The reduction is most in the plots burned annually. The importance of this in favoring pine reproduction has been shown by Little and Moore (1950). They show that the number of pine seedlings per acre increases from around 510 in the unburned controls to 3490 and 4660 in the plots burned annually and every two years over a ten year period. In another set of plots, 94 per cent of the pine seedlings of the 1947 crop were found where the duff was no more than ¼ inch deep, and no seedlings were found where the duff exceeded a depth of 1½ inches.

It should be pointed out, perhaps, that two roles of the litter layer which are important in most forests, that of increasing infiltration rates and of reducing surface runoff, are relatively unimportant in the pine region. This is due to the high porosity of the soils and the low topography of the area. There is some evidence, however, that in the uncut portions of the most frequently burned plots there is a slight decrease in the infiltration rate of the soils (Burns 1952). This factor should receive careful study in the long-term experiments getting under way at the present time.

The litter layer as a habitat for insects should not be ignored. Some species are important in the pollination of

the blueberry and cranberry crops that are important in the region. Others are pests of varying degrees of importance. The influence of the decrease in litter on these insect populations should be given careful study.

The reduction in shrub cover is a second important effect of prescribed burning. When stands are burned at three year intervals or oftener, cover by this layer is reduced roughly by one-half. (See data on open space in Figures 2A and 3). Since the shrub layer competes with arborescent seedlings, a reduction of this layer through prescribed burning would give the young pine seedlings a short period of reduced competition.

The pronounced reduction in the shrub cover and the practical elimination of the litter may have a substantial effect on the amount of rainfall interception. With these layers diminished, more water will undoubtedly get to and into the ground and thus appreciably increase percolation to the water table.

Much more difficult to evaluate are the effects of the shift in relative importance of the shrub species. *Vaccinium vacillans* is apparently affected less by burning than *Gaylussacia baccata,* the other important upland shrub. The result of this difference is a shift in the relative importance of these species with increased burn frequency (Figure 3). Little is known to the authors of the relative palatability of these two species to deer, the major game animal of the area. This factor might be worthy of investigation. Perhaps of more immediate importance however, is the possible importance of this shift to the cranberry and blueberry industries. *Vaccinium vacillans* is much more closely related genetically to these two crops than is *Gaylussacia baccata.* Investigations should be initiated into the relationships of these two species with the cultivated ones in regard to pollination problems. Also of interest is the question as to whether these two species have major differences in their tendency to harbor pathogens capable of transfer to cultivated plants.

The consumption of the accumulated fuel on the forest floor is a very important result of the practice of prescribed burning. This fuel accumulation presents a constant threat of uncontrolled fires which result in considerable damage to the forest. The reduction of this fuel is brought about by the periodic consumption of the litter and shrub layers. Although many of the shrub species produce vigorous sprout growth the season following winter burning, this type of growth is not as combustible as the dead stems which begin to accumulate after the third year in some species.

In silvicultural practice, a period of prescribed burning is usually followed by the cutting of the overstory. A few seed trees of pine are often left to insure a seed source in case of accidental destruction of existing seedlings (Little and Moore 1950). This removal of the tree canopy permits the young pine to begin a period of rapid height growth, sometimes as much as six feet in two years, which is far above the usual rate of growth in the region.

During this transition from seedling to young tree stage, because the young pines are highly susceptible to fire, all burning is discontinued in these areas until the pines make enough growth to put the major part of their canopy above the height of fire damage. Also during this period there is a thickening of the periderm and an increase in stem diameter, both of which increase fire resistance.

This phase of the silvicultural program produces considerable change in the ground cover in the more frequently burned plots. The large increase in herbaceous cover, the continued shift in dominance of shrub species, and the absence of tree cover characteristic of the period following cutting and cessation of burning create a considerable change in vegetation structure. It seems probable

that the hydrological relations will be altered the most during this lack of a true tree canopy. Heavy browsing of the young pine by deer indicates that this stage may be a favorable game producing vegetation type.

Due to the short duration (15 years) of the experimental silvicultural program, it is not possible to say what changes will occur in the ground cover as these young pine stands develop further. It seems probable that as the pine trees increase in height and form a relatively closed canopy, shrub cover will decline. It is part of the planned silvicultural program to begin periodic controlled burning (perhaps every three years) under the pine stands as soon as the trees reach a safe height. This, of course will further alter the shrub layer and keep fire fuels at a safe level. Later study will be necessary to determine the amount and composition of the ground cover that will exist under the mature pine stands.

## Summary

The effect of prescribed burning on shrub cover is to greatly reduce it. The practice affects all species but not all to the same extent. *Gaylussacia* species show the most pronounced changes.

The herbs and mosses in general increase in cover with increased frequency of burning.

Cutting the trees results in an increase in cover for the shrub, herb, and moss layers whether the areas have been burned or not, but the effects are greatest where the burning has been most frequent. In the moss layer, it is the lichens rather than mosses that increase with the increased light.

Cutting the trees causes a decrease in litter cover and cover of *Gaylussacia baccata*.

The importance of the changes in the lower layers of vegetation resulting from prescribed burning lies in their effect on: tree reproduction (pine being favored); rainfall interception; animal populations; changed habitat for insect fauna; plant disease reservoir; and the problem of fire control.

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# HOME RANGE AND MOVEMENTS OF THE GREEN FROG, *RANA CLAMITANS*[1]

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## INTRODUCTION

The significance of "home range" as a biological concept in the life histories of animals was greatly clarified by Burt (1943) who pointed out that the home range is the area over which an animal normally travels in search of food. Breder *et al.* (1927) showed that green frogs had favorite spots near which they stayed and to which they returned when taken away. They demonstrated homing ability of green frogs by tagging and moving them from place to place, the maximum distance in their experiments being about 110 meters. My observations are in agreement with the results of their experiments, but because no artificial conditions were created by displacement of animals, some information about the causative factors involved in movements and the nature of the home range was obtained.

It is a pleasure to acknowledge my indebtedness to Frederick H. Test for directing this study, to James A. Gregory for permission to use the study area, to Eugene P. Odom and Edward J. Kuenzler for critical reading of the manuscript.

### *Study Area*

This study was made during 1948 and 1949 on a site located approximately five miles northwest of Ann Arbor, Michigan. Here a somewhat L-shaped plot which extended over 27,000 square meters (6.7 acres) was studied (Fig. 1). It was restricted to the vicinity of a clear, actively flowing stream which entered an artificially constructed lake about 20 meters south of the study site. This lake, although a breeding area for green frogs, was not included in the study area because its soft mucky bottom made wading difficult. The level of this spring-fed stream was fairly constant throughout the year except for the day or two following a downpour when it would get high and muddy. This gravel-bottomed stream rather regularly flowed over shallow rapids and into deep pools of an average depth of a half meter but which occasionally ranged upward to one meter. Its width varied from one to ten meters with an average about three meters. In 1949 the study site was expanded to include an abandoned meander located southwest of the stream (Fig. 1). It did not receive any water from the main stream but was supplied by springs and its flow was considerably slower than that of the stream. This permitted a luxuriant growth of vegetation consisting of *Nasturtium officinale, Elodea,* and *Sparganium.* In contrast, the main stream was relatively free of vegetation, having only widely scattered patches of *Nasturtium.*

The banks of the stream were somewhat steep and exposed, rising on the average a meter above the water. Primarily of loam, they bore patches of *Carex* and scattered *Eupatorium perfoliatum, Setaria glauca,* and *Solanum dulcamara.* Above the banks was a vigorous growth of *Poa.* On either side of the stream were widely scattered trees, primarily *Ulmus fulva, Salix, Crataegus, Acer saccharum,* and *Juglans nigra.* Level fields extending along the stream except on the eastern border where hills rose abruptly to about 25 meters. The study area was closed to the public and used for grazing

[1] This paper is extracted from a dissertation presented at the University of Michigan.

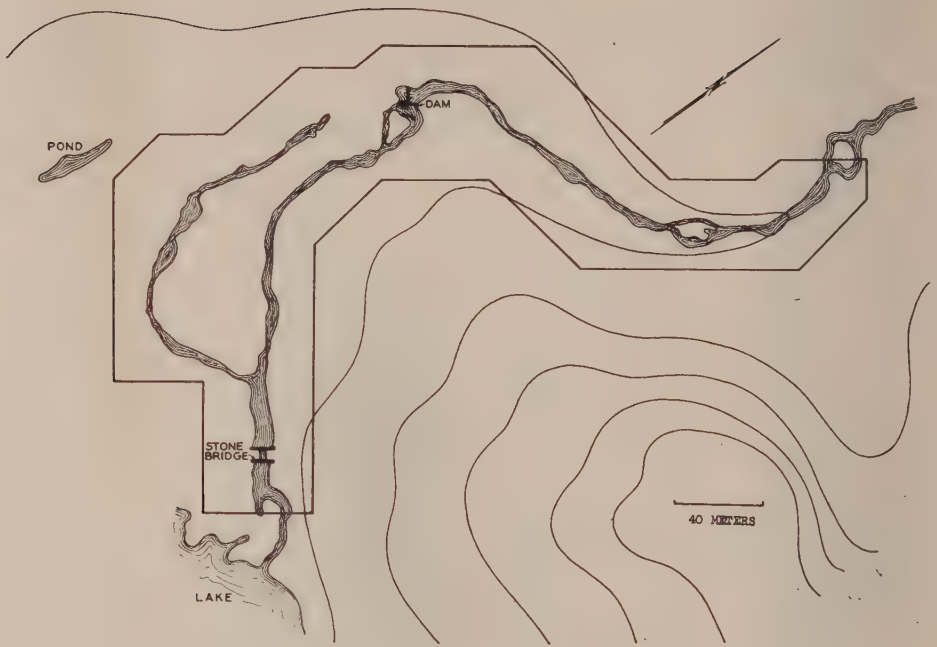


FIG. 1. Map of the study area. The contour lines are for a three-meter interval.

of cattle and sheep. No important disturbances were known to occur to the frog population.

The green frog (*Rana clamitans*) was undoubtedly the most common amphibian on the study area. Next in order of abundance were: bullfrog (*R. catesbeiana*), cricket frog (*Acris gryllus*), leopard frog (*R. pipiens*), pickerel frog (*R. palustris*), wood frog (*R. sylvatica*), and American toad (*Bufo terrestris*). The total number of captures of the three last-mentioned species was only fourteen.

### *General Methods*

Each week the entire study area was systematically censused. When I saw a frog, I cautiously approached and generally captured it by a quick thrust of my hand. Nocturnal capture of frogs was remarkably easy since they made no attempt to avoid the approaching light. A headlight, operated by four flashlight batteries, proved to be satisfactory illumination for measuring specimens and writing data, but was inconvenient for locating frogs because much turning of my head was required. For searching, a hand lantern, operated by a six-volt battery, provided sufficient light to see frogs easily.

Each frog was marked for future recognition by cutting its toes with scissors, care being exercised that the web between them was not seriously injured. The method of marking proved to be very satisfactory. It is discussed in another paper (Martof 1953).

As an aid in studying the movements of frogs, the study area was surveyed by compass and markers were placed at ten-meter intervals forming a grid, with numbers assigned to one ordinate and letters to the other. Originally the markers were wire but later were replaced by wooden stakes because cattle easily trampled the wire markers. By observing the distance north or south and east or west from the nearest marker, the location of each frog was rather accurately obtained.

In addition to the above mentioned

data, measurements were taken from snout to vent and of the tympanum diameter of each captured frog. Also the sex of each adult specimen was noted at the time of capture, the tympanum measurement proving useful for those individuals whose sex was questionable, particularly the recently matured frogs. Because the nature and intensity of ventral markings and dorsal coloration varied considerably among individuals, general color patterns and markings were noted. All these characteristics provided a check on the identity of recaptured specimens.

Each frog was released at the place of capture, and information pertaining to the nature of its habitat was recorded: kind and density of vegetation, and distance from water or shore. General weather data such as sky condition, precipitation, wind velocity, air and water temperature, and humidity were taken. In addition, date, time, behavior, and general remarks were recorded. At no time were frogs removed from the area and care was continuously exercised to preserve the naturalness of the study site.

In this study 1221 green frogs were marked. Sixty seven per cent (824) of these frogs were captured but once, while five per cent (61) were captured five or more times and one half per cent (7) were taken from 8 to 14 times. A total of 2056 captures was made.

## Season of Activity

Green frogs emerged from hibernation in the last week of March in both 1948 and 1949, at which time the mean daily temperature had risen above 40 degrees F., or what is more important, the maximum temperature was above 60 degree F. for three or four days. However, it was not until early April that they were found in sizable numbers. Rainfall, as well as temperature, played an important role in causing the frogs to emerge from hibernation. It was difficult to evaluate the significance of each, especially from field observations, because rainfall usually accompanied high temperatures. Since water has a high specific heat, warm rains were very effective in releasing frogs from their hibernacula. This close association of temperature and rainfall in stimulating amphibian activity in the spring was earlier noted by Wright (1914), Cummins (1920), and Blanchard (1930). Since green frogs, as well as other amphibians, hibernate under variable conditions, it is probable that the period of warm weather necessary to arouse some of them would be longer than for others. Accordingly, emergence from hibernation would be expected to be a somewhat gradual process. This is true for the green frog but not for other anurans, which breed shortly after coming from hibernation. Perhaps an hormonal influence is responsible for their early mass appearance.

Green frogs started to go into hibernation in the last two weeks of October. By mid-November none were found in the study area. At this time the mean daily temperature registered about 40 degrees F. and the maximum temperature had not gone above 60 degrees F. for several consecutive days. The last green frog taken in 1948 was on November 13, the last one in 1949 on October 29. Thus the frogs had an activity period which extended over approximately 220 days, with no signs of aestivation. There are, however, reports taken in the vicinity of Chicago (Pope 1947) of green frogs being active during mild weather in the winter months, especially near springs.

No special attempt was made to locate frogs in hibernation, although early in the spring they were observed hibernating in the mud or debris on the stream bottom in water about a meter deep. Judging from the numerous records of frogs taken in the same sites before and after the winter season, one may conclude that an individual usually hibernates in its home range (Fig. 3).

## Habitat and Time of Daily Activity

To understand the daily movements of the green frog it is first necessary to dis-

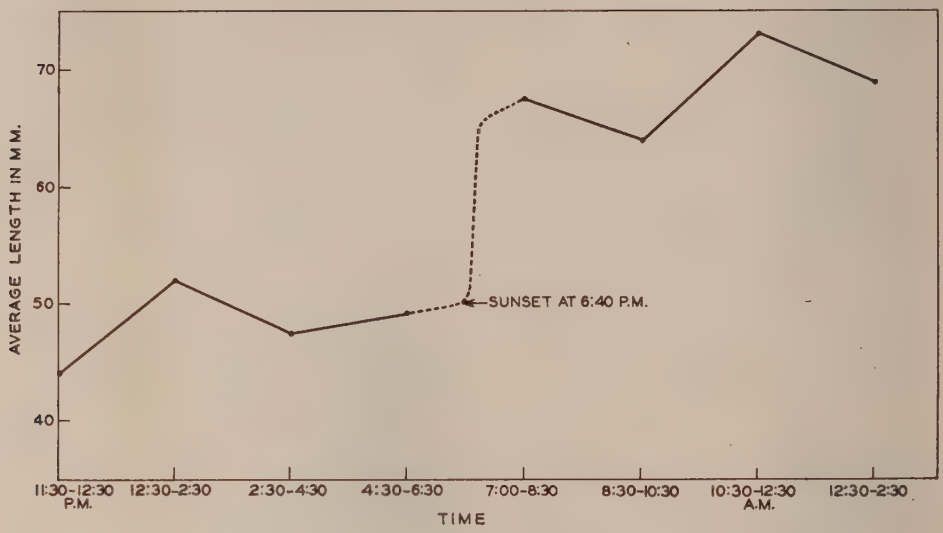


FIG. 2. Average bi-hourly lengths of 198 frogs taken Sept. 17-18, 1949. Dotted line is derived from actual observations.

cuss its habitat. In the literature the green frog is generally referred to as an aquatic species and thus similar to the bullfrog (Ruthven *et al.* 1928). In this study, it was found to be primarily an inhabitant of the banks of streams, being adept at climbing even almost vertical banks and rocks. This habitat, the banks and the area just beyond the banks of streams, was peculiar to the green frog only. Other kinds of frogs were sometimes found there but these individuals proved to be few and transient. Appropriately green frogs could be called "bank frogs," for their nightly return to the bank was most regular. Although their habitat for feeding is terrestrial they are highly dependent upon water as a refuge from the desiccating effects of the air, low temperatures, and enemies.

Normally all green frogs spent the daylight hours in the water or within about a meter of it. The smaller individuals being in shallow water situations were more available for capture than were the adults, many of which were in rather inaccessible places, such as muskrat burrows, root entanglements undercut by the water, and similar locations. However, on dark, cloudy days many large and some small individuals were active, being found on the banks and beyond—about three or four meters from water. This was also the usual condition during the night.

Thus the habitat of a green frog is directly related to the time when it is available for capture. Whereas the smaller frogs were clearly more available for capture during the day than were the large ones, the collections made at night were mainly composed of large frogs. In spite of the greater difficulty involved in locating small frogs during both day and night, because of their size and preference for more densely vegetated places, it became clear that they simply were not as available at night as in the daytime. Special efforts to find them even in locations where they had been observed in daylight were not very successful, despite the fact that most frogs seen were captured, and many others were found by carefully groping for them in depressions and vegetation along the sides of the stream. On the other hand, the adults were active at night foraging on the banks, where they were readily found.

In order further to study the time of activity of frogs of different sizes, comparable night and day collections were examined. Several times in June-September, 1949, the area was censused twice in each day, once in the daylight and again after dark. This was the objective of each weekly tour of the area but because of low temperature, heavy rains, and the great abundance of frogs at certain times, it was not always attained. Therefore, only those periods with equivalent night and day collections each covering the entire study area, were analyzed. These periods were selected in order to eliminate such factors as the uneven distribution of adult and subadult habitats resulting in uneven distribution of different-sized frogs in the area.

In these selected periods when the area was censused in the daylight and after dark the rate of capture of frogs was practically the same, 7.045 and 7.059 per hour, respectively. Because of the nearly identical rate of capture for day and night collections, a realistic comparison of these periods could be had only after they were made equivalent to one another. Therefore, the night tallies for each size group were multiplied by 1.194 which was the ratio of the actual time spent collecting during the day, 46.7 hours, to that at night, 39.1 hours. These adjusted values are given in Table I as the equivalent night captures. Next the percentage of all captures made during the day and also the night (using the equivalent data) was ascertained for each size group. The direct relationship of the size of a frog to its period of activity is obvious. The large individuals are chiefly nocturnal, the very small ones diurnal, and the middle ones (about 50 to 70 mm. in body length) are equally active during the night and day.

TABLE I. *Size distribution of day and night captures at Loch Alpine in June-September, 1949*

| Size, mm. | Captures | | Equivalent | Percentage of capts. | |
|---|---|---|---|---|---|
| | Day | Night | Night capts. | Day | Night |
| 25-35... | 32 | 0 | 0 | 100 | 0 |
| 35-45... | 90 | 18 | 21 | 81 | 19 |
| 45-55... | 56 | 33 | 40 | 65 | 35 |
| 55-65... | 60 | 48 | 58 | 51 | 49 |
| 65-75... | 51 | 64 | 76 | 40 | 60 |
| 75-85... | 27 | 64 | 76 | 26 | 74 |
| 85-95... | 13 | 47 | 56 | 19 | 81 |
| 95-105.. | 0 | 2 | 2 | 0 | 100 |
| Total... | 329 | 276 | 329 | | |

The time of day in which the shift from small to large frogs occurred is shown in Figure 2. The average body lengths of all captures made Sept. 17 and 18, 1949 were obtained for two-hour intervals. The frogs captured before sunset averaged 45-50 mm. in length; those taken after sunset had average sizes of about 65-70 mm. Usually no collecting was done during the one-half hour at dusk because of the inadequate lighting, making it diffcult to observe and measure frogs. The conspicuous presence of large frogs on the banks shortly after sunset was repeatedly observed. There the frogs stayed until about sunrise when they gradually withdrew to the vicinity of the stream.

*Factors Limiting Daily Activity*

(1) As already discussed, light was a major factor which determined the time of activity of green frogs, the small individuals being primarily diurnal and the large ones nocturnal.

(2) Since temperature plays a very important part in the activities of cold blooded animals, it was not unexpected to find a close correlation between night activity and this factor. Because of the drainage of cold air into the stream valley, relatively low temperatures were often obtained at night. It was noticed that when the air cooled to lower than 60 degrees F. the frogs would withdraw from the banks. Some lingered in the water along shore, but later when the air temperature was well below 60 degrees F. and that of the water was usually higher (61-63 degrees F.), frogs were

often observed on the bottoms of the deeper pools. As the water cooled to 60 degrees even these disappeared, probably into mud on the bottoms of the pools. Later in the season, after about mid-August, a few frogs were found out of the water when the air temperature was as low as 56 degrees F. Perhaps a seasonal adjustment of the temperature threshold, related to the intrinsic changes preparing frogs for hibernation, occurs.

Not only did the 60-degree limit hold for nightly activity but also in daylight as well. Throughout the two seasons the great majority of frogs were taken when the air temperature was well above 60 degrees F., some were captured at temperatures of 55-60 degrees, and a few at 53 degrees. Three frogs, taken when water temperatures were 45-50 degrees F., were first seen either on the bottom of deep pools or were accidentally captured as I groped in bottom vegetation and other places likely to be inhabited. None were very active even when captured.

(3) The influence of precipitation was most striking. Immediately before, during, and after precipitation (rain or drizzle) green frogs were hyperactive. Instead of confining their foraging to the three or four meters adjacent to the streams they were then taken as far as 20 meters away. Undoubtedly these trips enabled frogs to learn their way around in the area and thus permitted them to return more or less directly to their home sites. The activity demonstrated before a rain was no doubt greatly stimulated by the decrease in light that generally accompanied precipitation.

In view of the extensive movements of green frogs during rainy weather it first seemed surprising that night activities should be so restricted when there was no precipitation. Generally the wet-bulb temperature was then only a few degrees lower than the dry-bulb reading, a heavy dew was the usual nightly phenomenon. Consequently, high relative humidities prevailed near the ground, approximating the atmospheric conditions of humidity during precipitation. A solution to the interpretation of this behavior is suggested by the work of Adolph (1932) who showed that frogs and toads obtain water by absorbing it through their skin from contact with damp objects, as damp ground. He pointed out that it may be doubted whether frogs absorb water from an atmosphere saturated with water vapor except under special conditions when the vapor tension of the surrounding air was greater than that of the water-permeable surface of the animal. Adolph (1933) also showed that frogs exposed to saturated air under uniform temperatures continued to lose water by evaporation. "The reason for this is one that holds for all organisms and tissues; it is that the frog is continually producing heat, thus raising its temperature above that of its surroundings, hence enabling it to evaporate water by raising the dew-point of the air in contact with its surface." Until a method has been devised to measure the vapor tension of a living animal, the influence of humidity cannot be satisfactorily understood.

Thorson and Svihla (1943) experimentally demonstrated that amphibians vary considerably in their ability to survive loss of body water and found a direct correlation between the amount of body water that could be lost and the natural habitats of the species studied. Although they did not study *Rana clamitans,* their work suggested that it is not able to survive much loss of body water and accordingly cannot range far from a constant source of water.

(4) There seemed to be considerable variation in the activity periods of individuals. This was shown by the irregular intervals between captures of the same frog. A possible explanation is found in the observations of Fischer-Sigwart (1897) that frogs and toads were inactive after eating large food items, often retiring to places of concealment and com-

ing out only when stimulated by hunger. Thus periods of comparative rest are required after periods of voracious feeding.

## Home Range

The daily activities of a green frog were confined to a comparatively small area. Considering all recapture records, about one-half indicated movements less than one meter, and five-sixths of them showed movements less than ten meters. Frequently a frog was found several months or even a year later in exactly the same spot or within five to ten centimeters of it. Twelve frogs captured at the beginning and near the close of the study period almost two seasons later had an average maximum movement, exclusive of breeding trips, of almost ten meters. These movements in the home range were usually related to night foraging. To establish in an area and not to wander far was the typical behavior.

There is much variation in the shape of the home range. A typical one is shown in Figure 3. Eight of the 14 times that this frog was captured, it was within a radius of 0.3 meter of the same spot.

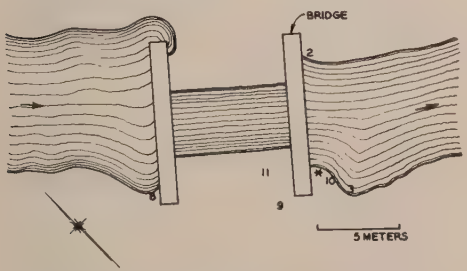


Fig. 3. Typical home range of a male green frog (49-77 mm.) near the stone bridge at Loch Alpine. Note preference for a particular spot shown by an asterisk.

| *date* | |
|---|---|
| *1. Sept. 4, 1948 | 8. July 2 |
| 2. Oct. 25 | 9. July 29 |
| 3. May 6, 1949 | 10. Aug. 7 |
| *4. May 13 | 11. Aug. 27 |
| *5. May 21 | *12. Sept. 3 |
| *6. June 3 | *13. Oct. 1 |
| *7. June 9 | *14. Oct. 10 |

Twice it was taken on the gravel road over the stone bridge about 2-3 meters away; both of these records were made at night. Of the other four captures, two were somewhat downstream (0.5 m. and 1.5 m.) from the above mentioned spot, one was made directly across the stream, and the other was on the opposite side of the stone bridge. At no time was the frog captured more than ten meters from its choice spot.

The home ranges of green frogs varied considerably in size. Some, as the one shown in Figure 4, restricted their activities to a small area of about 20 square

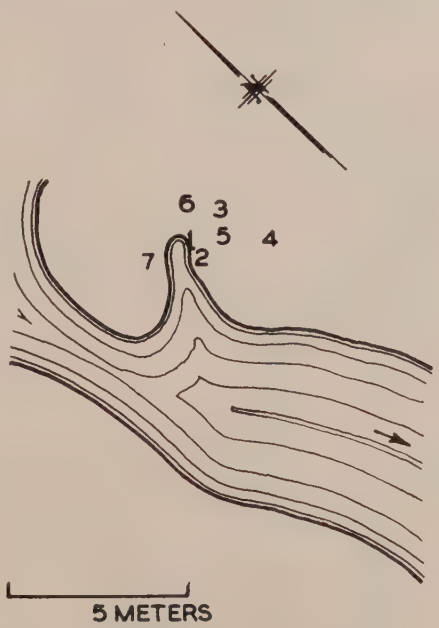


Fig. 4. Small home range of a female (78-81 mm.) at Loch Alpine.

| *date* | |
|---|---|
| 1. May 20, 1949 | 5. Aug. 13 |
| 2. May 28 | 6. Aug. 28 |
| 3. July 23 | 7. Sept. 3 |
| 4. Aug. 6 | |

meters; others showed more extensive movements (Fig. 5), ranging over about 200 square meters. Home ranges were measured with a planimeter and interpreted to include the area inclosed by the points of capture. Situations that were never inhabited by green frogs were excluded when they were located within the

FIG. 5. Large home range of a female (87-89 mm.) at Loch Alpine.

| | *date* |
|---|---|
| 1. June 18, 1949 | 5. July 22 |
| 2. June 26 | 6. July 30 |
| 3. July 2 | 7. Aug. 12 |
| 4. July 16 | |

area outlined by the points of capture. Therefore, the measurements included in this paper are considered to be minimal. Of the 43 records of individuals with five or more captures in their home ranges (not activity ranges), the average home range was 61 square meters. Sub-adults in general had smaller home ranges than adults but much variation was noted (Table II).

No attempt was made to analyze the factors regulating the shape and size of the home range of green frogs but very

TABLE II. *Size of home ranges of green frogs*

| | Number | Size of home range in sq. meters | | | |
|---|---|---|---|---|---|
| | | Min. | Max. | Mean | Stand. dev. |
| Subadults.... | 14 | 20 | 110 | 52.7 | 24.2 |
| Adults..... | 29 | 20 | 200 | 64.8 | 35.8 |
| All Frogs.... | 43 | 20 | 200 | 60.9 | 33.1 |

probably the physiography of the stream and banks, the density of the population, and the availability of food were contributing elements.

Even subadults had restricted home ranges, several small individuals being observed for an entire season in the same area. The home ranges first established by subadults generally were not as permanent as those demonstrated by large frogs and included shallow water with a dense growth of vegetation (*Carex, Eleocharis, Elodea, Nasturtium*). Usually these were abandoned as the frogs reached about 60-75 mm. in length, when they moved to situations in which the water was deeper and the aquatic vegetation not so dense. Presumably the protection afforded early by plants was later provided in part by deep water.

Subadults did not always move directly to the adult habitat. Some frogs were observed to vacillate between two locations and not to use the intervening area at all, as shown by the typical example in Figure 6. By noting the water contours it can be observed that one location is near shallow water and the other beside deep water; wavering of the above type was noted for frogs 60-75 mm. in body length, which were maturing or recently matured individuals attempting to establish in deep water. Apparently the distance between subadult and adult ranges determined whether these vacillating movements would occur, for only when a frog established in a nearby place did it return to its former location. The greatest distance observed between the

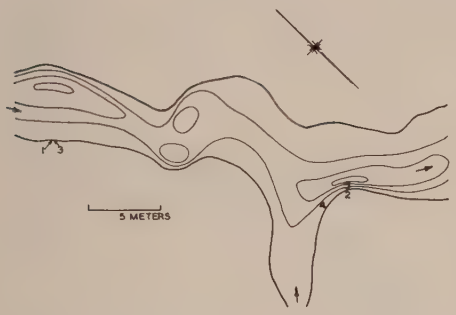


FIG. 6. Vacillation of a recently matured male (67-76 mm.) at Loch Alpine between its subadult and adult habitat niches. Lines in the stream on this map represent a nine-inch interval.

| *date* | |
|---|---|
| 1. July 24, 1948 | 4. Sept. 4 |
| 2. Aug. 21 | 5. May 6, 1949 |
| 3. Aug. 21 | |

two parts of such double ranges was 25 meters. It first seemed strange that this frog did not establish on the opposite shore from its subadult habitat, where seemingly favorable conditions existed. However, it was later noted again and again that most green frogs showed a strong tendency to stay on the same side of the stream.

Figure 6 is also of interest because it shows that a green frog can quickly find its way about in the nearby region. On August 21 it made the journey from one range to the other in less than 56 minutes. As it was not observed between captures, the actual time involved was not known. Apparently green frogs are well acquainted with their immediate surroundings. According to Yerkes (1903) they have adequate memory to perform such a feat; he found that they could run a familiar maze after a lapse of a month. When disturbed, green frogs always sought refuge in the nearby water and never did they move along the sides of the stream to avoid capture. Thus it was most unlikely that the above-mentioned frog was driven from one range to the other. The behavior of the individual shown in Figure 6 also suggests that a frog may set out with a definite objective rather than being forced along by other frogs, current, or some other environmental feature.

The diet of the green frog (Hamilton 1948) reflects its habitat but nowhere can one find direct reference to the bank environs as being the habitat for this species. As the frogs moved out onto the banks and beyond, they seemed to select the more exposed areas—rocks, paths, bare soil, overturned sod, logs, large branches, dried cow dung, places where the grass was closely grazed, etc. From these vantage points they very probably awaited their prey, although in about 200 hours of night collecting none were seen in the act of feeding.

At night the green frogs were very alert and sat with their heads high. As I approached they carefully watched my light but usually made no attempt to escape, rather appearing to be attracted to the light. Some individuals, even after they had been marked, would placidly sit nearby, apparently fascinated by the light. Others, even after having been examined, unhesitatingly jumped at the light and hit it with quite an impact, behaving much as some positively phototactic insects in a similar situation. Because of this lack of fear of the light and the greater nocturnal activity (hence availability), much night collecting was done.

### MOVEMENTS OUTSIDE HOME RANGE

In addition to daily movements there were those which involved greater distances and which may be classified as being associated with (1) growth and subsequent maturation, (2) breeding activity, and (3) overwintering.

Of the 397 frogs recaptured, 91 (23 per cent) showed movements that were not associated with their home range. The most extensive of these, involving the largest number of green frogs, were made by newly transformed individuals moving outward from the lake, where larval development occurred. Large numbers of them invaded the shallow water along the stream as they attempted to establish

themselves. This dispersion was clearly responsible for the comparatively large turnover of recently transformed individuals observed in the study area. Even though but 43 per cent of the movements outside the home ranges were attributed to maturation, this process certainly resulted in much greater changes in the composition of the populations than is indicated by this amount. Since the above data were derived from recaptures, they primarily show the movements of established individuals from subadult to adult ranges and not the more impressive dispersion of newly transformed frogs. At times of metamorphosis, young frogs were taken in places where previously none were observed and where no tadpoles were found close by at any part of the season. Seventy-two per cent of these movements were upstream, away from the breeding area.

An interesting feature of this dispersal was that no newly transformed frogs were seen actually moving from the breeding sites, even though several special attempts to locate them were made both by day and night. However, because of the greater abundance of unmarked animals found after rains early in the season of metamorphosis and the smaller numbers after later rains, it was concluded that most dispersion was accomplished in rapid moves during times of rain. Not all movements of these young frogs were directly correlated with rainfall, for several individuals were later recaptured farther upstream when no rain had fallen in the intervening period. Thus it was concluded that major shifts in population occurred during precipitation but that individual adjustments sometimes took place at other times. The factors determining which individuals dispersed and which remained behind are not understood. Some were observed to maintain home ranges close to the breeding site throughout the period when hundreds of newly transformed frogs moved through the area. Perhaps the first to reach a vacant spot stopped there, while others kept moving till they found an unoccupied place.

Winter freezes, spring thaws and floods effected some important changes in the habitat of the green frog; banks were eroded even to the point of caving in, trees fell into the stream creating new ponds, and some old ponds filled in while others were deepened by the swift waters. These alterations were followed by adjustments in the frog population. Not only did frogs which had been established nearby move into places recently made suitable for occupancy but, just as frequently, unmarked individuals were captured there. In addition to these modifications of the habitat, changes may have occurred directly to the frogs. It is very probable that some were dislodged from their hibernation sites and transported downstream by the hurrying waters, for five of the six examples of major movements associated with the overwintering period were downstream. All these frogs were subadults, suggesting that adults either hibernated in more protected places or else promptly returned to former home sites early in the spring. Since overwintering movements constituted only about six per cent of all recorded major movements and involved subadults solely, I thought that these frogs probably were not established prior to hibernation.

The most extensive movements of adults were those to and from the breeding areas. About 45 per cent of all observed major movements were associated with reproductive behavior and of these, approximately 60 per cent were upstream, away from the breeding areas. As pointed out earlier, most of these recovered individuals returned to their former home sites when the breeding season was over. Roughly 80 per cent of the adult frogs that were captured in the spring and again in the fall occupied their same home ranges. Figure 7 shows an example of an established individual which joined the breeding congress (in

abandoned meander) and then returned to its original home range. It was difficult to determine precisely how many did

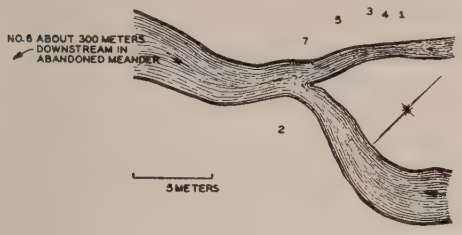


FIG. 7. The home range and breeding movements of a recently matured male (55-79 mm.) at Loch Alpine.

*date*

1. June 3, 1949
2. June 19
3. July 3
4. July 16
5. July 30
6. August 19
7. Sept. 18

return from the breeding areas because there was no evidence that certain females ever left their places along the banks of the stream. Judging from the known records, females were about twice as consistent in returning to their home sites as were males. The following factors undoubtedly were operative in producing this difference: (1) the females were gone from their home ranges for a much shorter time (about a week compared to over two months for male frogs), hence the chance that other frogs would take over their temporarily abandoned sites would be decreased; (2) in the shorter period the extent of physical change in the vegetation, contours of the stream, depth of water, and other environmental features would be less.

Most females and some males which did not return to their former home sites after breeding were located farther downstream. Almost all records indicated that these frogs were not established prior to the reproductive season, but upon return from the breeding area again attempted to establish themselves as they moved upstream. It seemed as though they established in the first unoccupied site encountered. Consequently, the later-returning males encountered a greater density of frogs near the breeding site, and many of them were forced to occupy places more distant from the breeding ponds than did the females.

Another kind of movement related to breeding was that of males in the breeding areas, where the frogs in one pond moved to another for about a week and then returned (Martof 1953). The large number of egg clusters found in the visited pond immediately afterward suggests that this movement may have occurred to meet reproductive demands. Drought, too, as occurred in 1948 (Martof 1952), caused the drying out of the above-mentioned ponds and thus forced the breeding frogs to seek larger, more permanent ponds.

## DISCUSSION

The evidence presented in this report indicates that green frogs have a temperature sense with a threshold of response just above 60 degrees F. Actually, Morgan (1922) demonstrated that the skin of a frog has "well-defined receptors for heat and for cold." She worked with both *R. pipiens* and *R. clamitans,* unfortunately making no distinction between them in her data. The frogs responded to temperatures above 102-110 degrees F., rarely attained in the Ann Arbor area, by vigorous jerking and twisting of the legs and body, apparently striving to escape. At temperatures below 50-59 degrees, the frogs became rigid, their muscles tense. Between these two limits they appeared to be tolerant of changes in temperature. It is the lower range which plays an important role in the natural life of the green frog by limiting activity and stimulating the internal changes prerequisite to hibernation (Holzapfel 1937).

The way in which frogs responded to temperature is directly related to light. When Torelle (1903) placed frogs in warm air or water they moved toward the light, but in the same media at 46

degree F. they moved away from the light. Cole (1907) secured similar results when he placed a green frog in a dark box with a large and a small illuminated area at opposite ends. When a frog was cooled to 50 degrees F., it would move toward the smaller area, but when warmed above 68 degrees it immediately moved toward the larger one. Intermediate temperatures were not tested.

Thus a frog would move towards the light and emerge from hibernation when it was warmed above 55-59 degrees F., whereas in the autumn when temperatures fell below 60 degrees, it would move away from the light, into the mud and under the rocks on the bottom of the stream. If the animal happened to be some distance from water when a sudden drop in temperature occurred, it would be forced to hibernate under the litter (Bohnsack 1951) or wherever it happened to be when so conditioned as to be negatively phototactic.

Because of the physiological conditioning which is essential to hibernation (Holzapel 1937), changes may occur which bring about a lowering of the threshold at which frogs respond to low temperatures. This might explain the finding of some frogs late in the season when the air temperature was above 56 degrees F.

As I found *R. pipiens* at lower temperatures than *R. clamitans*, it is probable that the variation in the threshold temperatures (50-59 deg.) reported by Morgan reflects specific differences between them.

The close association of rainfall with moderate temperatures in the spring caused some concern among earlier workers as to whether humidity or temperature is more instrumental in effecting emergence from hibernation. Considering that high humidities prevail not only in aquatic but also in terrestrial hibernation sites during the winter and spring, it seems logical that temperature is the crucial factor. Because of the high specific heat of water, rains warm the hibernation sites (a temperature effect) and emergence takes place. In other words, rain accelerates the transfer of heat to the torpid animal. When the frog becomes adequately warmed, it becomes active and as it is then positively phototactic it moves out to start another season. On the other hand, cold rains do not cause emergence from hibernation.

This prompts a fuller consideration of the influence of rain, for it was found that green frogs occurred in larger numbers and at greater than usual distances from the streams during times of precipitation. The major factors effecting this greater activity are not clearly indicated but, very probably, an interaction of several is responsible.

The role of humidity in frog activity is of major importance, ranking with that of temperature. Shelford (1913) demonstrated a definite preference for moist air by *R. sylvatica*. Relative humidity is indicative of the rate of evaporation of body fluids of frogs. Thorson and Svihla (1943) found that a direct correlation existed between habitat preferences and the amount of body water that several species of amphibians could lose without forfeiting their vitality. The effect seen on green frogs under natural conditions when low relative humidity (high rate of evaporation) prevailed, as on warm clear days, was primarily restriction of activity to small individuals in shallow water or its immediate vicinity. Large frogs remained in situations where high humidities existed and where loss of body water was avoided. On the other hand, during most nights, when the relative humidity rose because of radiation of heat from the earth, the rate of evaporation of body water was reduced and the larger green frogs foraged on the banks and beyond, some distance from water. In cloudy, rainy weather the absolute humidity as well as the relative humidity increased, and at these times—even in daylight—green frogs moved to places more dis-

tant from water and were found in greater abundance than usual. Headlee (1917) presented data suggesting that an optimum humidity exists for each species of insect and for each stage of each species and that humidity directly affects metabolism. A similar influence is very probably experienced by green frogs.

Another factor promoting greater activity may be higher body temperature. During times of rainfall the relative humidity is higher. As a result, the rate of evaporation is lower, and the body temperature of the frog probably remains comparatively high, very close to the air temperature. During cloudy weather, the air temperature also remains relatively high, especially at night, because radiation from the earth is greatly reduced. Thus it is suggested that optimum humidity conditions along with optimum temperature conditions must exist in order to promote maximum physiological activity of green frogs.

It is possible that the lower light intensity occurring when the sky is overcast may also cause frogs to seek with greater vigor those places where there is more light. In other words, their phototactic tendencies may be accentuated causing them to move about more energetically and to go farther out beyond the banks to places which may be somewhat better illuminated.

Less likely, but possible, contributing factors in producing heightened activity are tactile stimulation by the falling raindrops and visual stimulation produced by the moving raindrops resulting in a frog's response to them as to elusive prey.

Another interesting result of this study was the discovery that the green frog changes from a diurnal to a nocturnal animal as it gets larger. Both physical and biotic factors may be involved. The small frogs preferred shallow water and dense vegetation, which are places generally affording more protection from predators, and foraged about more freely during the day. Their great surface area per unit of volume may force them to be more aquatic because of their comparatively great loss of body water due to evaporation when away from water. With increasing size there is a relative decrease in surface area and hence a lower rate of evaporation, with the result that the frogs become more and more terrestrial. However, their activities away from water are restricted to those times of relatively low rates of evaporation, during the night and times of rainfall. It is also possible that their requirements for ultraviolet, which is essential for growth (Brody 1945), force them to be diurnal.

On the other hand, the large frogs selected the deeper pools which usually did not have much vegetation. It was repeatedly observed that the adult green frogs used these pools primarily as refuges from their many terrestrial enemies. When in the water, adults usually swam directly to cover in the bottom mud or under rocks, and when they left these places they would swim directly to shore, seemingly making their exposure to aquatic predators, particularly fishes, as brief as possible. Many large frogs were observed to spend most of the day in protected places near the water's edge and in brush entanglements, roots of trees undercut by the water, muskrat burrows, and similar places. This suggests that they probably could not endure for any great length of time the rapid evaporation which occurred in the more exposed terrestrial habitat during the daylight hours but were forced to be active at night. It is also of interest that their major predators, garter snakes and herons, are chiefly diurnal.

It might be argued that the small frogs were forced to occupy habitats differing from those utilized by adults. Because of their cannibalistic tendencies, the adults would thus impose a direct selection upon small frogs so that mainly those which established in places other than the adult habitat survived. This is not entirely true, because some small frogs were ob-

served to settle in typical situations for subadults which were in close proximity to adult habitat and still survive. Apparently this is possible chiefly because of the different periods of activity for small and large frogs. It appears that these two mechanisms, the habitat preferences and the different activity periods of adult and young green frogs, serve to moderate intraspecific predation.

Gause (1934) pointed out that two or more species with closely similar ways of life cannot coexist indefinitely in the same habitat niche, because one will inevitably prove more efficient than the others and will crowd out and eliminate its competitors. The native species of *Rana* are in little competition with one another because they have distinct niches and even distinct over-all habitat. The bullfrog is largely aquatic, and except during movements of adults to and from the breeding sites and during dispersion of newly transformed individuals, it infrequently goes more than a meter from water. The wood frog is sylvan, while the leopard frog is mainly a field dweller. The scarce pickerel frog was not observed enough to determine its habitat niche in this area. Therefore, the green frog being riparian does not compete with the other ranids.

## Summary

In 1948 and 1949, 2056 captures of 1221 green frogs were made on a site located near Ann Arbor, Michigan. All frogs were marked, examined, and released at the place of capture. Records were made of the behavior of each frog, location of capture, amount and type of vegetation, nature of substratum, temperature, and general weather conditions.

Green frogs came out of hibernation in the last week of March or the first week of April, when the mean daily temperatures were above 40 degrees F., and the maximum above 60 degrees for three or four successive days. They went into hibernation in the last half of October or the first half of November when the temperatures fell below the same levels.

The green frogs studied were strictly riparian except in the breeding season, with small and large individuals largely using different habitats. Small ones were established in shallow water which usually was provided with dense vegetation, and their foraging was chiefly along the nearby shore and during the daylight hours. In contrast, the large frogs preferred the vicinity of deeper pools, regularly moving up the banks and beyond to forage at night. This difference in time and place of activity which existed between large and small frogs serves to lessen intraspecific predation.

Practically all green frogs which were recaptured had definite home ranges within which they usually occupied certain small areas. The size of the home range varied from 20 to 200 square meters, with the average about 60. In general, the bigger animals had larger ranges but much individual difference was indicated. Adults returned to their home ranges even after extensive movements to the breeding areas, the females more regularly than males.

Daily activity was restricted by temperature. When the air was cooler than 60 degrees F., the frogs withdrew from the banks into the water and reappeared only when the temperature again rose above this level. Precipitation was also important in determining the activity of green frogs. It was found that frogs occurred in greater abundance and at greater distances from the streams during times of rain or drizzle.

In the winter and spring some hibernating subadults apparently were transported downstream by the high waters. However, most overwintering frogs were taken in the same places in which they were captured the previous year, indicating that they hibernate in their home ranges.

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# WATER RELATIONS AND CHLOROPHYLL CONTENT OF FOREST HERBS IN SOUTHERN WISCONSIN

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## INTRODUCTION

Many investigators have presented the results of studies concerned with differences between sun and shade plants. In most instances, the heliophytes (sun plants) are those which normally grow in full sunlight, while the sciophytes (shade plants) are those which grow in very dense shade, *Oxalis acetosella* being a favorite. These studies have been concerned with such characteristics as leaf morphology and anatomy; transpiration, respiration, and photosynthetic rates; pigment concentration, development of conducting system, osmotic value of cell sap, and water relations.

These earlier studies have dealt, in the main, with species which are radically different in that they reach optimum development in either bright sunlight or in very dense shade. The present paper, on the other hand, is concerned with a comparison of the species characteristic of several portions of the upland forest continuum in the prairie-forest border region of Wisconsin. This continuum is a lineal arrangement of forest stands which embraces the gradient from the pioneer forest stages, with their high light intensities, immature soils, and variable moisture conditions to the climax forests with their extreme shade, mature soils, and constant, abundant moisture conditions. The continuum index, which ranges from 300 to 3000, locates any given stand along the continuum.

The writer wishes to express his appreciation to Dr. John T. Curtis for suggesting the problem and for helpful advice and criticism throughout the study as well as in the preparation of the manuscript.

## LITERATURE REVIEW

No attempt is made here to review all of the literature pertaining to differences between sun and shade plants. Extensive summaries of various aspects of these differences may be found in Clements (1905), Warming (1909), Combes (1910), Hanson (1917), Burgerstein (1920, 1925), Maximov (1929), and Rabinowitch (1945).

The concentration of chlorophyll in sun and shade plants of the same species and its effect on the production of oven-dry matter was studied by Lubimenko (1908). In general, he found that shade leaves contain more chlorophyll per unit of leaf area and larger chloroplasts. However, sun plants contain more dry matter. He concluded that more light is needed for maximum dry-weight production than for maximum chlorophyll formation. Maximum dry-weight production in chlorophyll-poor plants occurs at or near full sunlight, but in plants rich in chlorophyll it takes place at much lower light intensities. In general, stems show less development in sun than in shade while roots show more. He believes that light also exerts an effect on assimilation, probably by influencing formation and destruction of enzymes.

Boysen Jensen (1919) studied *Sinapsis alba,* a heliophyte grown in full daylight, and *Oxalis acetosella,* a sciophyte grown in deep shade. He found that *Sinapsis* photosynthesizes and respires at approximately eight times the rate of *Oxalis*. Expressing the total increase in dry weight over a period of four weeks as average daily dry matter increase as a percentage of initial dry weight, he found a value of 15 per cent for *Sinapsis* and 2.1 per cent for *Oxalis*. Photo-

synthetic and respiration rates are equal in *Sinapsis* at a light intensity five times as great as that for *Oxalis*.

In the investigations of Dietrich (1926), heliophytes were found to transpire much more repadily than sciophytes on a unit leaf area basis, regardless of whether sun or shade individuals were used and of whether the experiments were conducted in sun or shade.

Huber (1924) worked with sun and shade branches of oak and measured the stem cross-section area of the active xylem per unit area of leaf surface. These values he compared with the transpiration rates. The transpiration rate of shade leaves was 60 per cent that of the sun leaves, but the active xylem per unit leaf area of shade branches was only 50 per cent that of the sun branches. Since more water passes through the xylem cross-section per unit time in the shade branches there is a greater resistance to water passage. Therefore, when more water is being lost through transpiration, the sun branches can overcome their increased resistance but the shade branches are unable to do this and consequently wilting occurs.

According to the investigations of Maximov (1938), sun plants do not exhibit wilting until 25 to 30 per cent of their turgid water content has been lost because the cell wall is very distended in the turgid condition and still remains elastic after a great decrease in volume of the cell. Shade plants, on the other hand, exhibit definite signs of wilting after losing only 2 to 3 per cent of their water content because the cell walls are not distended, even though under tension, and therefore collapse with slight decrease in cell volume.

In studying citrus trees, Monselise (1951) found the osmotic pressure of the cell sap to be 15 per cent higher in sun leaves than in shade leaves of the same trees.

## Methods

Selection of species and arrangement of data were greatly facilitated by the use of the upland forest continuum (Curtis and McIntosh 1951). Data for 96 upland hardwood stands in southern Wisconsin, for each of which a continuum index value had been determined, were utilized in the present study. The vegetational continuum was divided into nine equal-sized intervals (i.e. 300-600, 600-900, etc.), but, since no stands have as yet been found with a continuum index value in the 2700-3000 range, only the first eight intervals have been utilized. Thus, the 96 stands were divided into eight groups. Within each continuum interval, the average frequency, based upon 20¼ milacre quadrats per stand, of each herb species was then calculated. When the eight average-frequency values for a particular species were plotted against the continuum index, the interval in which that species reaches its optimum development became apparent. Throughout this paper "optimum development" refers to the peak of this average-frequency curve. Some of the species included, particularly some of the pioneer species, undoubtedly reach true optimum outside the limits of the continuum.

For the wilting studies, ten species were selected in each continuum interval, with the exception of the 600-900 interval, in which only six species were found to reach optimum development. Thus, 76 different species are included. The species selected within any one interval are among those which reach optimum development within that interval and are the ten which have the highest average frequencies there.

This method of species selection would have resulted in the inclusion of *Claytonia virginiana, Dicentra cucullaria,* and *Erythronium albidum* in the 2400-2700 continuum interval. Inasmuch as these species die down before the forest canopy has reached its maximum density, they are not considered to be representative of

the true shade vegetation. Consequently, these three species are excluded.

Since, as Livingston and Brown (1912) have shown, the water content of leaves declines during the day and increases at night, the weights of fully turgid leaves are best determined early in the morning during a period proceeded by a normal amount of precipitation. Eight forest stands, each representative of a different continuum interval, were selected. Each stand consisted essentially of undisturbed forest, but included small portions which had been recently cut. These stands were visited between the hours of four and seven o'clock (standard time) on consecutive mornings in early June. The presence of abundant dew on grass outside the stands served as additional assurance that the plants being studied were near full turgidity. The species studied in any stand are the ten which peak in the continuum interval to which that stand belongs.

A triple-beam balance was erected on a log or stump in the woods and sheltered from the wind. A sample of leaves from one of the ten species was collected from several individuals and weighed immediately. The leaves were then placed on logs, or other exposed positions and allowed to wilt, while samples of the other species were collected in like manner. When wilting was unmistakably evident the leaves were reweighed. They were later brought in to the laboratory for determination of the oven-dry weight. In most instances only the leaves were weighed, but in those cases (e.g. *Galium concinnum*) where the removal of enough leaves to give an adequate sample would have been so time-consuming that some water loss would occur before the weighing, a minimum of stems was included. Such species are indicated by an asterisk in the table.

Three additional species: *Fragaria virginiana,* a pioneer species; *Viola pubescens,* a climax species; and *Geranium maculatum,* a species which reaches optimum development near the middle of the continuum, but which occurs commonly throughout, were similarly sampled in all of the stands in which they occurred.

For the chlorophyll studies, five of the species used in each interval for the wilting studies, were chosen. These are the five with highest average frequency values which could be found growing undisturbed in the normal shade of the stand visited and also in portions of that stand which had recently been cut in light logging operations. Examination of the rhizomes and other underground parts of these plants were made in all cases where possible to insure that the herbs had been growing there before the canopy had been opened.

Eighty sets of leaf samples, consisting of leaves from forty species growing undisturbed in the shade and from forty series of plants of the same species which were undisturbed except for the recent removal of the tree canopy above them, were gathered in the same stands as were used in the wilting studies. Within each series ten samples were removed from as many leaves by means of a cork borer, each sample having an area of 65.0 $mm^2$. The larger veins were avoided. The ten samples were pooled and the chlorophyll was extracted quantitatively in acetone and then transferred quantitatively to ethyl ether. Determinations of the total chlorophyll content were made by means of the Evelyn photoelectric colorimeter, using a 660 filter, thus obviating the necessity of removing the carotinoid pigments.

The oven-dry weight of ten duplicate samples was also determined for each shade series.

After the chlorophyll content had been determined for all forty species, 15 cc. portions of the chlorophyll solutions of the shade series were simultaneously exposed to bright sunlight for a period of six months in test tubes placed on white paper. The total chlorophyll content was then redetermined.

The nomenclature used is that of Fernald (1950).

## Results

It was suspected that if any one species were sampled in several continuum intervals, variations in the characteristics under consideration would be highly likely to occur. In order to test this hypothesis, the three species discussed below were studied throughout those portions of the continuum in which they occur. These studies were confined to two characteristics: per cent of water loss before wilting and proportion of oven-dry matter in the leaves. No attempt has been made to distinguish between ecotype and ecad.

*Fragaria virginiana* is a distinctly pioneer species as is shown by its average frequency curve. That optimum development of this species lies outside the range of the forest continuum is strongly suspected. The decrease from 23 to 4 per cent in water loss before wilting is a most pronounced trend (Figure 1). Similar, but less marked, is the curve for proportion of oven-dry matter in the leaves (Figure 2).

*Viola pubescens,* a climax species, shows a similar curve for water loss before wilting. In the case of dry matter content, however, the downward trend is preceded by a slight rise.

*Geranium maculatum* was chosen as an example of a ubiquitous species, for, while its average frequency curve shows a pronounced peak in the 1200-1500 interval of the continuum, it occurs in 92 of the 96 stands which constitute the base of this study. The two curves for this species are alike in that no definite trend is apparent.

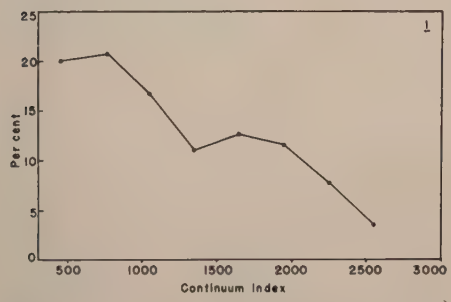


Fig. 1. Per cent water content lost before wilting. Averages of ten species per interval.

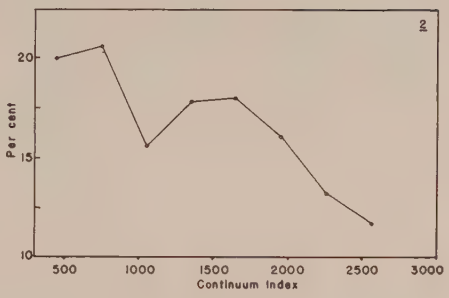


Fig. 2. Oven-dry weight of leaves as per cent of turgid weight. Averages of ten species per interval.

It is obvious from the fact that such curves show some trends, that a considerable difference might result in the values obtained throughout the present study if the species were sampled in stands selected at random. The samples were, therefore, obtained from stands belonging to the continuum interval in which the species reach optimum development.

In Table I are presented the values obtained for each of the 76 species studied. This table also serves to indicate the species studied and the continuum interval in which each reaches optimum development. In the first column is shown the percentage of water lost before wilting became apparent. These values were calculated by dividing the difference between the fully turgid weight and the weight at wilting by the difference between the fully turgid weight and the oven-dry weight. Within each continuum interval, the arithmetic mean was calculated for the ten species and the resulting values plotted in Figure 3. This curve shows a pronounced decrease from the pioneer to the climax portions of the continuum. The pioneer plants lose approximately 20 per cent of their total water content before they wilt while the climax species show signs of wilting when

TABLE I. *Species studied, arranged in continuum intervals of optimum development, with values obtained for the characteristics described in the text. Values in first two columns for species marked with one asterisk are based upon samples which included stems or woody stipes. Wintergreen species are denoted by two asterisks*

| Intervals and species | Water lost before wilting | Per cent dry matter | Dry weight of shade series | Chlorophyll in shade series | Chlorophyll in sun series | Chlorophyll after photodestruction | Chlorophyll per mg. dry leaf |
|---|---|---|---|---|---|---|---|
| | % | % | mg | ug | % | % | ug/mg |
| *300-600* | | | | | | | |
| Antennaria sp. | 18.6 | 17.7 | | | | | |
| Apocynum androsaemifolium | 21.3 | 19.4 | | | | | |
| Comandra umbellata | 15.7 | 19.1 | | | | | |
| Euphorbia corollata | 20.9 | 21.6 | 3.4 | 12.3 | 107.5 | 57.5 | 3.6 |
| Fragaria virginiana | 21.7 | 24.0 | 4.2 | 13.9 | 90.0 | 62.2 | 3.3 |
| Helianthus strumosus | 20.2 | 16.4 | 3.7 | 14.3 | 111.8 | 44.1 | 3.9 |
| Polygonatum canaliculatum | 18.8 | 18.3 | | | | | |
| Potentilla simplex | 12.4 | 22.1 | | | | | |
| Pteridium aquilinum* | 24.0 | 22.7 | 4.6 | 13.9 | 90.0 | 75.5 | 3.0 |
| Smilacina stellata | 26.1 | 18.8 | 4.1 | 22.5 | 80.8 | 67.8 | 5.5 |
| *600-900* | | | | | | | |
| Anemone quinquefolia | 23.0 | 19.3 | 4.3 | 17.5 | 96.5 | 26.0 | 4.1 |
| Gaylussacia baccata | 20.0 | 25.9 | 4.6 | 13.4 | 103.4 | 77.0 | 2.9 |
| Goodyera pubescens** | 22.1 | 8.4 | | | | | |
| Hieracium canadense | 21.2 | 21.4 | 4.5 | 14.6 | 95.0 | 67.4 | 3.2 |
| Parietaria pensylvanica | 15.5 | 20.2 | 3.2 | 13.4 | 89.7 | 58.6 | 4.1 |
| Vaccinium angustifolium* | 21.7 | 28.2 | 4.8 | 13.9 | 101.1 | 68.9 | 2.9 |
| *900-1200* | | | | | | | |
| Agrimonia gryposepala | 18.0 | 17.5 | | | | | |
| Aralia nudicaulis | 18.1 | 14.5 | | | | | |
| Arenaria lateriflora | 8.3 | 17.8 | 2.4 | 18.2 | 89.0 | 44.1 | 7.7 |
| Carex pensylvanica* | 30.6 | 26.7 | 4.0 | 14.3 | 107.5 | 80.6 | 3.6 |
| Circaea quadrisulcata | 13.8 | 10.2 | 2.5 | 9.8 | 76.6 | 53.1 | 4.0 |
| Geum canadense | 18.4 | 17.3 | | | | | |
| Lactuca biennis | 9.2 | 7.8 | | | | | |
| Lysimachia quadrifolia | 17.2 | 14.1 | | | | | |
| Phryma leptostachya | 12.0 | 14.2 | 2.1 | 13.9 | 92.2 | 63.3 | 6.5 |
| Smilacina racemosa | 21.4 | 16.6 | 2.4 | 16.2 | 74.3 | 74.3 | 6.8 |
| *1200-1500* | | | | | | | |
| Amphicarpa bracteata | 5.9 | 9.9 | 1.6 | 12.0 | 96.2 | 48.7 | 7.4 |
| Cypripedium calceolus | 15.4 | 11.9 | | | | | |
| Desmodium glutinosum | 13.5 | 14.0 | 1.9 | 13.9 | 95.6 | 54.4 | 7.4 |
| Eupatorium rugosum | 9.8 | 11.1 | | | | | |
| Galium concinnum* | 21.9 | 34.9 | | | | | |
| Geranium maculatum | 9.5 | 19.4 | 5.3 | 18.6 | 96.7 | 43.8 | 3.2 |
| Podophyllum peltatum | 14.4 | 19.8 | 4.8 | 22.2 | 76.4 | 91.0 | 4.6 |
| Prenanthes alba | 9.8 | 10.9 | 2.4 | 19.2 | 69.6 | 42.2 | 8.1 |
| Taenidia integerrima | 3.5 | 19.4 | | | | | |
| Veronicastrum virginicum | 7.7 | 26.3 | | | | | |

they have lost 3.5 per cent of their total water.

These results agree remarkably well with the observations of Maximov (1938). In comparing extreme sun plants with extreme shade species he found values of 25 to 30 per cent for the heliophytes and 2 to 3 per cent for the sciophytes. Since the present study is concerned with a narrower range of environmental conditions, the values might be expected to exhibit less variation. The extreme susceptibility of some climax species to wilting is easily observed in

| Intervals and species | Water lost before wilting | Per cent dry matter | Dry weight of shade series | Chlorophyll in shade series | Chlorophyll in sun series | Chlorophyll after photodestruction | Chlorophyll per mg. dry leaf |
|---|---|---|---|---|---|---|---|
| | % | % | mg | ug | % | % | ug/mg |
| *1500-1800* | | | | | | | |
| Aralia racemosa | 6.5 | 19.7 | | | | | |
| Athyrium filix-femina | 12.9 | 16.7 | 2.9 | 22.5 | 82.9 | 65.8 | 7.7 |
| Brachyelytrum erectum | 15.4 | 19.6 | | | | | |
| Galium triflorum | 4.5 | 14.7 | | | | | |
| Hackelia virginiana | 12.5 | 14.9 | | | | | |
| Osmunda claytoniana* | 17.1 | 23.2 | 2.9 | 18.6 | 108.3 | 43.8 | 6.4 |
| Panicum latifolium | 16.3 | 19.0 | | | | | |
| Pyrola elliptica** | 12.1 | 19.5 | 3.1 | 13.9 | 92.2 | 71.1 | 4.5 |
| Trillium grandiflorum | 15.2 | 12.5 | 2.2 | 18.6 | 62.8 | 59.5 | 8.4 |
| Uvularia grandiflora | 14.7 | 20.1 | 3.1 | 19.2 | 72.0 | 57.6 | 6.2 |
| *1800-2100* | | | | | | | |
| Actaea pachypoda | 8.7 | 17.0 | 2.6 | 16.9 | 50.0 | 41.8 | 6.5 |
| Aster macrophyllus | 11.1 | 12.1 | 2.7 | 18.6 | 89.3 | 76.0 | 6.8 |
| Galium circaezans | 9.9 | 17.1 | 2.1 | 15.4 | 72.0 | 64.0 | 7.5 |
| Hystrix patula* | 16.9 | 20.1 | | | | | |
| Maianthemum canadense | 14.9 | 17.3 | | | | | |
| Osmorhiza claytoni | 6.1 | 13.0 | 1.9 | 14.9 | 57.7 | 53.6 | 7.9 |
| Ranunculus abortivus | 16.5 | 17.3 | | | | | |
| Sanicula gregaria | 8.1 | 13.8 | 2.4 | 19.7 | 78.1 | 36.3 | 8.4 |
| Smilax herbacea | 12.8 | 16.0 | | | | | |
| Smilax tamnoides | 12.0 | 16.1 | | | | | |
| *2100-2400* | | | | | | | |
| Arisaema atrorubens | 5.6 | 9.5 | 2.0 | 19.4 | 39.7 | 19.0 | 9.9 |
| Asarum canadense | 7.3 | 12.0 | 2.6 | 16.9 | 84.5 | 78.2 | 6.4 |
| Cryptotaenia canadensis | 8.1 | 13.7 | | | | | |
| Hepatica acutiloba** | 7.1 | 22.2 | 4.3 | 22.2 | 62.5 | 79.2 | 5.1 |
| Menispermum canadense | 7.3 | 8.1 | | | | | |
| Mitella diphylla | 9.0 | 16.2 | | | | | |
| Osmunda cinnamomea* | 14.3 | 17.6 | | | | | |
| Polygonatum pubescens | 8.0 | 10.9 | | | | | |
| Thalictrum dioicum | 3.4 | 10.0 | 1.3 | 13.9 | 71.1 | 23.3 | 10.4 |
| Trillium flexipes | 8.0 | 12.0 | 2.6 | 23.5 | 52.3 | 29.4 | 9.2 |
| *2400-2700* | | | | | | | |
| Adiantum pedatum* | 3.3 | 22.1 | | | | | |
| Botrychium virginianum | 3.0 | 14.4 | | | | | |
| Galium aparine** | 3.1 | 14.2 | 1.7 | 13.2 | 74.4 | 25.6 | 8.0 |
| Hydrophyllum virginianum | 2.3 | 12.9 | 2.5 | 20.8 | 60.7 | 18.5 | 8.2 |
| Impatiens capensis | 1.9 | 2.9 | | | | | |
| Laportea canadensis | 1.6 | 12.3 | | | | | |
| Sanguinaria canadensis | 3.7 | 12.4 | 2.7 | 15.9 | 18.4 | 12.6 | 5.9 |
| Trillium recurvatum | 8.0 | 9.8 | | | | | |
| Viola cucullata | 5.7 | 5.1 | 2.2 | 19.7 | 53.9 | 43.0 | 8.8 |
| Viola pubescens | 3.7 | 11.1 | 2.5 | 17.9 | 30.2 | 50.0 | 7.3 |

the field by picking *Impatiens, Laportea,* and *Sanguinaria.*

The amount of oven-dry matter in the leaves was calculated as a percentage of the fully turgid weight. These values are presented in the second column of the table. The average value for each continuum interval was plotted against the continuum index and the resulting curve is shown in Figure 4. Again, the values are found to decrease from the pioneer species to the climax species. A difference of approximately 67 per cent occurs between the two ends of this curve. These results agree with those of Geneau (1892) and of Lubimenko (1908) in that they

show considerably less dry matter in the shade species.

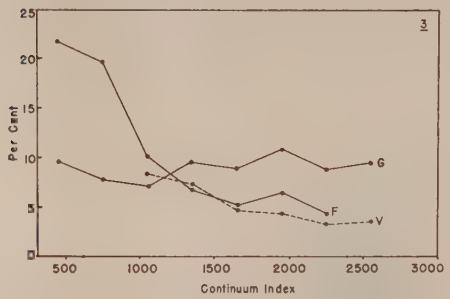


FIG. 3. Per cent water content lost before wilting for three representative species: *Fragaria virginiana, Geranium maculatum,* and *Viola pubescens.*

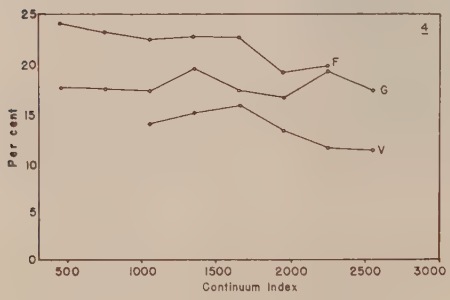


FIG. 4. Oven-dry weight of leaves as per cent of turgid weight for *Fragaria, Geranium,* and *Viola.*

Results similar to those in Figure 4 are obtained in the case of oven-dry matter per unit area, as determined on the basis of five species per continuum interval (Figure 5). A difference of approximately 50 per cent between the pioneer and climax species is apparent. Geneau (1892), comparing the leaves of sun and shade individuals of four species of herbs, found an average difference of 51.5 per cent for this same character.

The table also includes the results of the other studies with five species per continuum interval. In the fourth column of this table is shown the amount of chlorophyll, in micrograms per square centimeter, present in the shade leaves of each species, each series consisting of ten 65.0 mm.$^2$ samples from as many leaves.

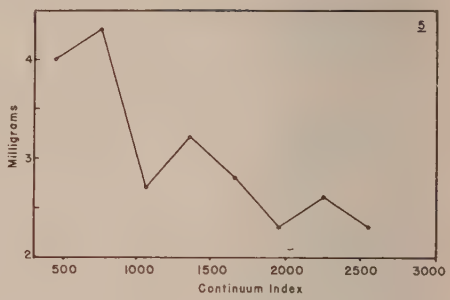


FIG. 5. Oven-dry matter per 1.0cm.$^2$ in leaf samples of shade series. Averages of five species per interval.

Arithmetic means of these values are plotted in Figure 6. Although there is considerable variation, it is readily apparent that the climax species contain more chlorophyll than do the pioneer species.

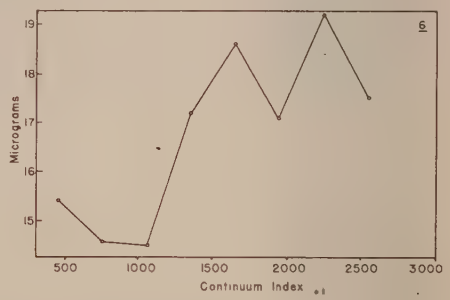


FIG. 6. Chlorophyll content per 1.0 cm.$^2$ in leaf samples of shade series. Averages of five species per interval.

An extreme difference between pioneer and climax species is shown in the case of the chlorophyll content of sun versus shade individuals (Figure 7). Those species which show optimum development in the pioneer portion of the continuum retain approximately 96 per cent of their chlorophyll content when the tree canopy is removed, while the chlorophyll content of the climax species is reduced by one half. This is easily observed in the field in the leaves of such species as *Sanguinaria canadensis* and *Viola pubescens,* which assume a pronounced yellow color in sites where the canopy has been removed.

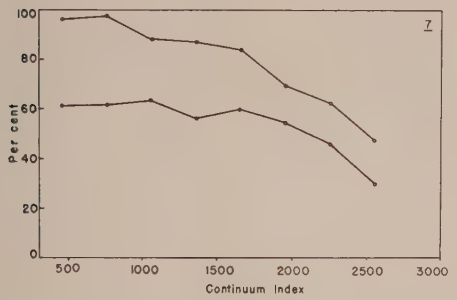


FIG. 7. Chlorophyll content of sun series as a percentage of that in shade series (upper curve). Percentage of chlorophyll retained in ether solutions of shade series after exposure to bright sunlight (lower curve). Averages of five species per interval.

Examination of underground parts, in all cases where possible, was undertaken to ensure that the plants growing in bright sunlight had been there before the cutting and thus could be considered genetically similar to the replicates still growing in shade. Observed differences between these replicates, therefore, are resultants of environmental change. As early as 1904, Boodle showed that young leaves are plastic; *i.e.* similar young leaves become mature sun leaves if grown in bright sunlight, or develop into characteristic shade leaves if grown in shade.

Decolorization of chlorophyll by bright sunlight is twice as rapid in the case of climax species as it is in pioneer species (Figure 7). Since no determinations were made of chlorophyll *a* : *b* ratios, it is not known whether this considerable difference is due to variation in quantities of chlorophyll *b*. However, since chlorophyll *b* is said to be much more susceptible to photo-oxidation than chlorophyll *a* (Strain 1949), and to be present in greater proportion to *a* in shade leaves (Rabinowitch 1945), this assumption seems reasonable.

While the curves in Figure 7 are alike the values for the ether solutions are noticeably lower. This difference might be expected from the remark of Rabinowitch (1945) that chlorophyll is less stable to light *in vitro* than *in vivo*.

The average amounts of chlorophyll per unit of dry matter contained in the shade series is shown in Figure 8. Although the trend is conspicuous, it is not believed that these values necessarily indicate a greater efficiency of the chlorophyll of pioneer species. Since much of the food synthesized in the leaves may be translocated to other parts of the plant, and since no measure was available regarding the amount of food translocated, it seems best to resist any tendency to draw such conclusions. Hesselman (1904) has shown that while most species have high photosynthetic rates in the spring, the measured rate drops, frequently to zero, in the case of forest herbs as a dense forest canopy closes above them. This measured rate seems to be the excess above the compensation point.

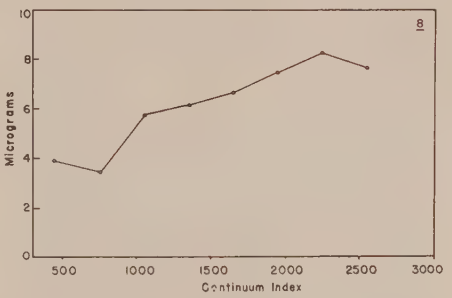


FIG. 8. Amount of chlorophyll per milligram of dry leaf matter in shade series. Averages of five species per interval.

An additional item of interest is the osmotic pressure of cell sap. No determinations of this characteristic were made in this study. However, twenty-five species for which sufficient data are available to yield average frequency curves, are included in the tables of osmotic pressure determinations made by Harris (1934). Within each continuum interval the osmotic pressures were averaged for the species which reach optimum development there. Two of the intervals lack species entirely. From the curve plotted in Figure 9, a decreasing trend

is readily apparent, even though so few species are included.

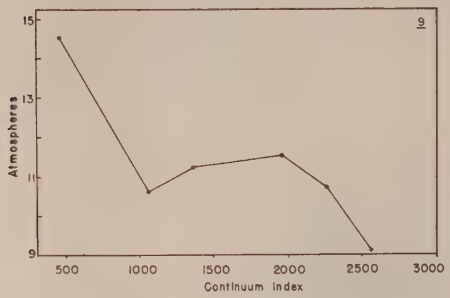


FIG. 9. Osmotic pressure of cell sap expressed from leaves (data from Harris 1934). Averages of 3, 6, 4, 3, 3, 6 species, reading from left.

There is no assurance, in this case, that the determinations were made on samples gathered in sites of optimum development. Descriptions of collection sites are given in Harris' tables, however, and any determinations based upon specimens from obviously non-optimum sites were not included in calculating the average osmotic pressure of a particular species.

## DISCUSSION

Previous studies have tended to show pronounced differences between heliophytes and sciophytes, but they have not indicated clearly whether these are differences of degree or of kind, as for example, in the case of leaf anatomy. If the extreme differences between sun and shade plants are differences of degree, species of intermediate sites may be expected to be intermediate with regard to these characteristics. That such is, indeed, the case is evidenced by the results of the present study. The curves are generally definite trends showing a gradual transition from one end of the continuum to the other.

Only one sharp break is apparent in most of these curves, usually occurring in the 1200 portion of the continuum. That this break can be correlated with density of the forest canopy is evident from field observation, although measurements adequate for comparison are not available at present. At this point along the continuum, the canopy density is approximately 85 per cent, a seemingly critical value for many species. For example, a curve of commonness of white oak (*Quercus alba*) seedlings, plotted against density of canopy, shows consistently high values until the canopy reaches a value of 85 per cent. At this point the curve drops abruptly to values near zero.

Reference has been made throughout this paper to light intensities. Light is not considered the sole determinant of the differences found in this study. Rather, being easily measured, it is here used as an index of the whole range of environmental conditions which may influence vegetation and which may be influenced in turn by the density of the canopy.

That considerable differences exist between plants characteristic of different habitats has long been recognized. Heretofore only the extremes have been compared inasmuch as it has been difficult to determine with sufficient reliability which species best represent the various intermediate phases of the vegetational complex. Since the present study is concerned only with the vegetation under a forest canopy (sciophytes in a broad sense), it does not cover the range of environmental conditions of previous investigators. It is expected that extension of the study to include plants of non-forested environments may show the existence of even greater differences.

## SUMMARY

The upland forest continuum in the prairie-forest border region of southern Wisconsin has served to delimit the forest herbs into eight groups, each characterizing a different phase of the vegetational complex within the forest.

Ten species per continuum interval were studied with regard to per cent of water content lost before wilting and

amount of oven-dry matter in the leaves as a percentage of the fully turgid weight. The resulting curves indicate a declining trend from pioneer to climax vegetation within the limits of the continuum.

In similar manner, but using five species per continuum interval, curves are presented for the following characteristics (with the trend indicated): chlorophyll content per unit leaf area (ascending), over-dry weight per unit leaf area (descending), chlorophyll retained in leaves after removal of forest canopy (descending), and chlorophyll content per unit of dry leaf weight (ascending).

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# A FIELD STUDY OF TEMPERATURE REGULATION IN YOUNG WHITE PELICANS, *PELECANUS ERYTHRORHYNCHOS*[1]

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The desert animals of southwestern United States are faced with extremes of heat and aridity surpassed in few parts of the world. Intense solar radiation, daytime temperatures above 40° C., soil temperatures above 55° C., and the absence of fresh water over vast areas combine to create severe biological problems during much of the year. Many desert vertebrates avoid this hostile physical environment by their nocturnal habits. Most of the other species go underground or otherwise seek shade during the hottest parts of the day in spring, summer, and early fall, thus avoiding solar radiation. A few species of birds, however, because of the location of their breeding sites, remain exposed to the direct rays of the desert sun all during the day. Conspicuous among these birds are the white pelicans (*Pelecanus erythrorhynchos*) which nest on bare sand bars at the south end of the Salton Sea, a large saline lake located 200 feet below sea level in the Colorado Desert, Imperial County, California.

This pelican colony is the most southerly one west of the Rocky Mountains. It was established shortly after the Salton Sea was created by the flood waters that flowed from the Colorado River into the Salton Sink in 1905 and 1906 (Grinnell 1908), and it has been the subject of an illustrated popular article (Walker 1943).

The colonial nesting of the white pelican made it possible to obtain temperature measurements from a large sample of young birds and to compare the behavior of many individuals under similar extreme conditions, thus offering a favorable opportunity for the study of temperature regulation in a wild vertebrate under natural conditions.

## METHODS

The principal observations on which the present paper is based were made on May 30 and 31, and June 17, 1952, although intermittent observations and censuses have been made over a number of years. All the body temperatures were taken during the May visits. The study on June 17 was devoted to observing the behavior of the undisturbed birds through a 20X telescope. The cloacal and gular temperatures of the birds and the air and water temperatures were measured to the nearest tenth of a degree centigrade with a mercury thermometer. As indications of relative age, we used development of down and a simple linear measurement: tip of bill to end of pygostyle with the bird in a prone extended position. Temperatures were measured during the middle of the afternoon and again during the middle of the night. The rookeries were left undisturbed between 5:30 p.m. and 10:30 p.m.

The remarks on food habits are based on regurgitated fish which were identified by Boyd W. Walker of the Department of Zoology, University of California, Los Angeles.

## RESULTS

The measurements of cloacal temperatures of young pelicans under various environmental conditions are summarized in Figure 1. We have divided the young into two size classes: less than 16 inches in length, and more than 16 inches in length. The former

[1] These studies were aided in part by a contract between the Office of Naval Research, Department of the Navy and the University of California (NR 160 171).

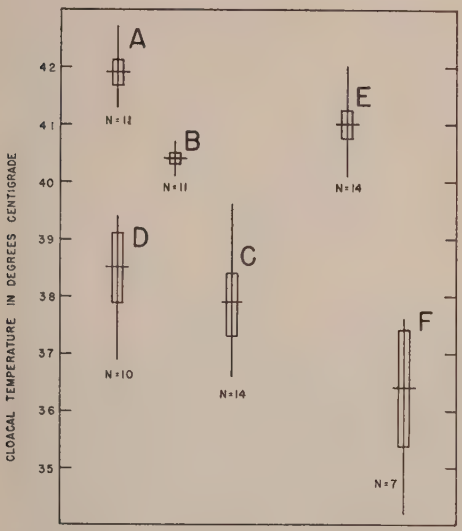


FIG. 1. Body temperatures of young white pelicans. The vertical lines indicate the range; the horizontal lines indicate the mean (M); and the rectangles indicate the interval $M + 2\sigma_M$ to $M - 2\sigma_M$. Units A to D represent groups of downy young 16 inches or more long; Units E and F, naked young less than 16 inches long. A and E show temperatures of dry young during the middle of the afternoon; C and F show temperatures of dry young between 10:30 p.m. and midnight; B shows temperatures of dry young taken between 4:00 and 5:00 p.m.; and D shows the temperatures of wet young taken during the middle of the afternoon.

were partly or wholly naked; the latter were completely covered with down. A well marked diurnal temperature cycle was present in both classes. There was no overlap in the ranges of day and night temperatures for either class. The difference between mean day and mean night temperatures for the downy young was 4° C., and for the naked young, 4.6° C. At night the mean body temperature (36.4°) of the naked young was significantly lower than that (37.9°) of the downy young ($P < .02$). This indicates an increase in regulatory capacity with age, perhaps related to growth of down.

During the hottest part of the day the mean body temperature of the naked young was lower than that of the downy young. This difference, which is statistically significant ($P < .01$), is probably due to the fact that until we entered the rookeries the naked birds had been shaded by their parents, while the downy ones had been exposed to the sun.

Between 4:00 and 5:00 p.m. (P.S.T.), when the intensity of the sunlight had diminished but the air temperature was essentially unchanged (35° C.), the body temperatures of the young pelicans were significantly lower than those measured earlier in the afternoon (Fig. 1). We interpret this to be an indication of the importance of solar radiation in causing an elevation of body temperature.

In the Salton Sea pelican colonies, which are entirely unshaded by vegetation, the primary problems of temperature regulation, both before and after hatching, relate to the prevention of overheating, rather than the prevention of cooling. Incubation and brooding of the naked young does occur at night, but during the day the adults shade the eggs and naked young by standing between them and the sun. Usually, the adults face away from the sun. Each time we approached a pelican rookery, the adults observed our approach with obvious uneasiness, but did not take to the air until we were almost in the rookery. Some of the birds with naked young stayed in the rookery even while we were working there. As soon as we entered the water to leave, the adults returned almost en masse. The reluctance of the adults to leave the nests and the rapidity with which they returned after having been disturbed may be related to the critical necessity of their providing shade for eggs and young. The intensity of the solar radiation is such that temporary departure of the adults during the day sometimes has fatal effects on the nestlings. Wetmore (1921) records similar fatalities caused by heat in heron and ibis rookeries from which the adults had been driven.

The shielding of the eggs and nestlings from the intense desert sun places on the adults a severe heat load which they meet by energetic panting, the effectiveness of which, as will be discussed below, is increased by the large gular pouch.

The ability of the white pelican to fish at night (Lamb and Howell 1913) and the fact that both sexes incubate (Bent 1922), make it convenient for eggs and young to be attended continuously during the day. At night many of the adults left the rookery. The few adults that remained were brooding naked young or incubating. Until the young birds are large enough to walk about, they are dependent for shade on the appropriate orientation of the adult birds. However, when the young are 16 or more inches long they may actively seek out the shade provided by the adults. As they grow larger and more independent, the young no longer stay with the adults continuously. They aggregate in groups, the location of which varies with the time of day and temperature.

On the afternoon of May 30, a moderately warm day by local standards (32-36° C.), the larger downy young birds formed a loose aggregation in the center of the rookery. In response to the disturbance caused by our activities, they huddled close together. At night, we found them organized in several closely packed groups of 30 or more individuals. On the afternoon of June 17, during which the environmental temperature varied between 37 and 41° C., the young birds formed loose groups, either in the water or at the water's edge. Some swam in the shallow water off the shore, some stood in water 8 or 10 inches deep, and others sat or stood on the wet sand. A few adults also stood or floated in the shallow water where they occasionally fed their young.

The significance of the behavior of the young in entering the water is indicated by the temperatures of the wet downy young shown in Figure 1. These birds were 25 to 30 inches long (as were many of the dry downy young measured). They had taken to the water to avoid us. We chased them for about 200 yards into a shallow inlet where we captured them and took their temperatures. All had been struggling violently to escape us. Nevertheless, evaporation from their wet down and conduction to the water had reduced their temperatures markedly (water temperature 33.9° C., air temperature 34° C.). The mean temperature of these wet birds was 3.4° C. lower than that of dry birds of comparable size (Fig. 1).

Further evidence concerning the effectiveness of the evaporation of water from the down of the young pelicans is supplied by our observations on the rate of reduction of body temperature when violently panting birds were wetted. During these observations the air temperature varied between 33 and 35° C. and the water temperature was 29.2° C.

A downy young 16.5 inches long with a cloacal temperature of 41.0° was crouching in the sun panting rapidly, apparently almost prostrated by the heat. We sprinkled it with water, and in one minute its temperature fell to 40.6°. At the end of three minutes its temperature was 39.9° and its panting had stopped. After its down dried out, the bird's temperature began to rise and five minutes later was 40.9°.

A 25-inch bird with a cloacal temperature of 41.4° was placed in water a few inches deep. It scrambled about and became thoroughly wet. After 90 seconds it stopped panting, and 4 minutes from the time it was placed in the water it began to shiver. Its cloacal temperature at this time was 40.1° C. The shivering may have been evoked by the rapid fall in temperature rather than by the depressed body temperature.

A 27-inch bird had its cloacal temperature reduced from 40.6° to 39.7° during two minutes in the water, and a 22-inch bird had its cloacal temperature reduced

from 40.3° to 39.6° during a stay of three minutes in the water.

When the environmental temperature approximates or exceeds body temperature, birds can lose heat only by evaporation of water from pharynx and respiratory tract. The powerful fluttering of the gular pouch of various pelecaniform birds in hot weather is a matter of common observation. Finley (1907), Behle (1944), and others have briefly commented on it in the white pelican.

The fluttering of the gular pouch of young pelicans is as evident as that of the adults. In both young and adults the thin translucent gular sac is highly vascular. When the birds are under heat stress, the vasodilatation of the gular blood vessels is conspicuous, even from a distance of several feet. The flut-

FIG. 2. A group of young white pelicans on the Salton Sea rookery during the middle of a warm day in June, showing the characteristic gular fluttering. Note the open mouths and distended gular pouches. The rapidity of gular flutter is indicated by the blurred pouch of the bird in the right foreground.

tering of the highly vascular pouch should facilitate evaporation on its moist inner surface and so afford an effective mechanism for cooling the bird's blood.

It is possible that the gular movements are not a result of rapid inhalation and exhalation. The glottis is relatively anterior and is clearly visible in the open mouth of a panting bird; movements of air into and out of the respiratory tract would not necessarily cause the observed rapid shaking of the gular skin—one partly naked nestling fluttered its pouch 255 times per minute. A mechanism such

as this for evaporating water by movements of a thin moist membrane should require less energy than the panting of most birds and mammals which involves movements of the whole thorax.

The effectiveness of this mechanism is indicated by the rapidity with which the fluttering of the pouch reduces the gular temperature. In one instance the gular temperature of a 29-inch bird was reduced from 41.0 to 38.5°C. in one minute of gular fluttering. The gular pouch of the newly hatched young is both relatively and absolutely much smaller than that of the older birds and probably is a less efficient cooler. This is borne out by the differences between gular and cloacal temperatures in the two size classes; the smaller birds showed a difference of 1.3°, and the larger showed a difference of 2.7° C.

Occasionally young pelicans, while standing or floating in the water, slowly immersed their bills and then raised them out of the water and resumed their gular fluttering. They did not appear to be drinking for they did not elevate the bill or make swallowing motions. This wetting of the outside of the pouch almost doubles its effective cooling surface.

Young pelicans occasionally die from overheating despite their mechanisms for dissipation of heat. They frequently regurgitate partly digested food when they become excited, and our activities caused this to happen a number of times. In one instance, a young bird 23 inches long regurgitated several fish that stuck in its pouch so that gular fluttering was prevented but its breathing was not stopped. We found this bird 7 minutes after we entered the rookery. It was motionless and breathing heavily. Its cloacal temperature was 44.0° C. We removed the fish from its pouch and throat and it immediately began to flutter its pouch. We put it into the water to see if it would recover and then turned our attention to other birds. Eighteen minutes later we returned and found it still in the water. Its movements were shaky and uncoordinated and its temperature had fallen to 37.7°. It died shortly thereafter.

A feature of pelican morphology that should contribute to the prevention of overheating is the enormous development of the air sac system. The unusually extensive superficial air sacs covering the ventral surface, shoulders, and neck of the white pelican (Richardson 1939, 1943) provide an effective insulating layer that should reduce the rate of acquisition of heat from the ground.

## Discussion

The ability of young pelicans to meet successfully the severe temperature conditions that prevail in late spring and early summer on the islands in the Salton Sea results from an interplay of physiological, behavioral, and morphological attributes.

The labile nature of the body temperatures of young pelicans enables them to establish a favorable difference in temperature between body and air during both day and night. During the day their elevated body temperatures allow them to lose some of their heat passively to the environment even when air temperatures are as high as 41 or 42°C. At night, their depressed body temperatures favor a low rate of passive heat loss to the relatively cool environment. The temperature of nestling pelicans varied over a range of 7.8° C. during a period when the environmental temperature varied only through 10.5° C. Even while the downy young were active during the day, their temperatures ranged through almost 6° C., depending upon whether they were wet or dry and upon the intensity of solar radiation.

The behavior of the adults and the young birds allows the latter to avoid direct insolation and to use the nearby water to wet themselves. The morphology of the gular pouch provides an effective means of evaporative cooling, and the extensive system of superficial air sacs provides a layer of insulation.

Nestling pelicans pant almost without interruption for many hours on hot days. Their metabolic water and the tissue fluids of the fish they eat are certainly important sources, possibly the only sources, of the water they evaporate. Although there is abundant observational evidence that gulls, petrels, and penguins drink sea water (Murphy 1936: 337), we have not seen pelicans drink the water of the Salton Sea which, while of about the same salinity as sea water, has different ionic concentrations.

Adult pelicans have opportunities to drink fresh water. The occurrence in the material regurgitated by the young birds of fresh-water fish (carp, *Cyprinus carpio,* and bluegill, *Lepomis macrochirus*), as well as fish from the Salton Sea (mullet, *Mugil cephalus;* desert pupfish, *Cyprinodon macularius;* and mudsucker, *Gillichthys mirabilis*) shows that the adults regularly fish in the irrigation system of the nearby Imperial Valley.

The large gular pouch and extensive air sac system of pelicans, which we have considered only with regard to heat regulation, are undoubtedly primarily significant in other respects. The use of the gular pouch by pelicans in fishing is generally known and is certainly its primary function. The role of the superficial air sac system, while not obvious in the surface-feeding white pelican, undoubtedly functions as a shock absorber in the brown pelican that plunges into the water to catch fish.

The utility of the pouch for heat regulation appears to be a case of preadaptation that makes available an external evaporating surface greater, both absolutely and relatively, than that possessed by any other bird. The extensive air sac system, whatever its primary function, furnishes an insulating layer of air that serves to cut down rate of heating from the substratum.

## Summary

In the deserts of southwestern United States white pelicans are among the few birds that remain exposed all day to the direct rays of the sun. Observations and measurements of body temperature were made on birds of this species in the rookeries on the unshaded sandbars at the south end of the Salton Sea in the desert region of southern California. Both naked and downy young have well marked diurnal temperature cycles with the mean night temperatures more than 4° C. lower than the mean day temperatures.

The primary temperature problem faced by the young birds is the avoidance of overheating. During the day the the adults shade the smaller young, but the larger young are exposed to the intense radiation of the sun. During the heat of the day the downy young form loose groups in the shallow water near shore. The mean body temperature of swimming young birds is more than 3° C. lower than that of dry young of similar size. When downy young are wetted, their body temperatures fall as much as half a degree centigrade per minute.

Both young and adults flutter their gular pouches almost continuously during the day. The evaporation of water from the large vascular gular pouch plays a major role in pelican heat regulation.

The capacity of the young to tolerate changes of as much as 5° C. in body temperature contributes to their ability to withstand high environmental temperatures and intense radiation.

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# PLANT COMMUNITIES OF OKLAHOMA LAKES[1]

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## Introduction

The first artificial lake in Oklahoma was constructed by the city of Ardmore in 1894. In 1910 this lake was enlarged to its present size. Since 1910, the construction of artificial lakes has continued at an accelerated pace, particularly during the years from 1930 to 1940. By 1947 there were 188 lakes with a total surface area of 187,722 acres and 71,000 farm ponds with an area of 60,000 acres. "Combining these farm pond areas with the areas of the artificial lakes indicates that a little over one-half of one per cent of the land of Oklahoma is covered by artificial impoundments" (Oklahoma Planning and Resources Board 1947). The largest artificial lakes in Oklahoma are Texoma (93,080 acres), Grand (46,300 acres), and Salt Plains (10,700 acres). Lake Texoma is the ninth largest reservoir in the United States, both in surface area and total capacity.

At the present time, Oklahoma ranks third among the states in the total surface area of its artificial lakes (Brill 1952). The per cent of the total area of some of the larger states covered by inland water in 1940 was as follows: Florida, 7.3; Louisiana, 6.9; Minnesota, 4.8; New York, 3.3; Michigan, 2.1; Texas, 1.4; Oklahoma, 0.9. At this time Oklahoma ranked eighteenth in the list of states. It should be pointed out, however, that the position of the state in this respect should have improved somewhat with the recent increase in the number of large impoundments.

The construction of artificial ponds and lakes has presented many opportunities for botanical investigation, especially for studies on the invasion of plants, the rate of plant succession, and the kinds of plant communities in new impoundments. In the management of these impoundments many problems have also developed, particularly on the relation of higher plants to the production of fish, migratory waterfowl, and aquatic mammals and to the control of mosquitoes. This investigation was initiated with the objectives of capitalizing on the above opportunities and of obtaining information of value in solving the above problems.

Lakes for investigation were selected from every section of the state with as diverse physical, chemical, and biotic conditions as possible (Fig. 1). Fifty lakes were visited but the report is based on thirty-two lakes which were studied during the summers of 1948, 1949, and 1950. The only natural lakes investigated were four ox-bows of the Red River, in southeastern Oklahoma, and four playas in the Oklahoma Panhandle. Artificial lakes were studied in all parts of the state except the Panhandle, which possessed only one lake, nearly dry at the time of the study.

The survey of each lake involved the history of its construction and previous management, the position of drift lines, erosion scarps, summer pool levels, the current pool level, and the kinds of plants and plant communities with reference to water levels. No attempt was made to obtain quantitative data on the plant communities and no data were collected on habitat factors except for depth of water.

Except for plants without flowers or fruits, and except for certain well-known species, vouchers have been taken of all species encountered, and deposited in the Bebb Herbarium of the University of Oklahoma. The eighth edition of Gray's *Manual of Botany* (Fernald 1950) and

[1] Contribution of the Oklahoma Biological Survey, Dr. Carl D. Riggs, Director.

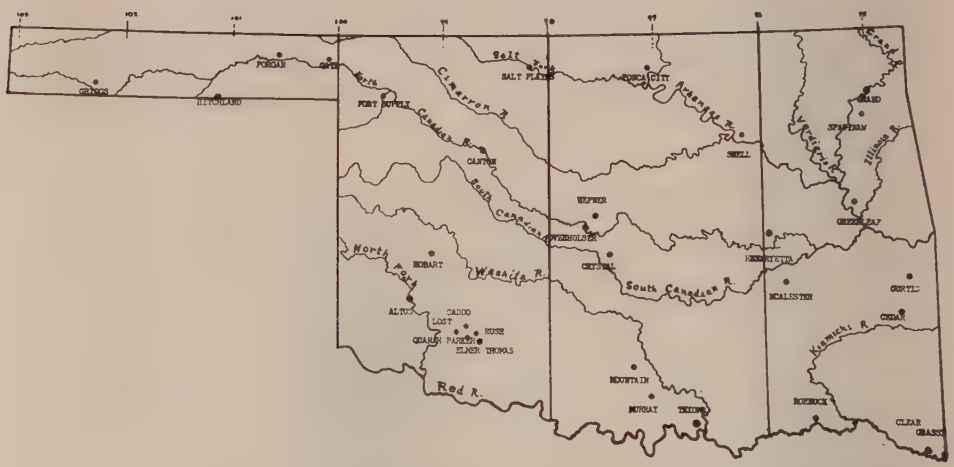


FIG. 1. Map showing location of Oklahoma Lakes in Panhandle, Western, Central, and Eastern sections (left to right).

the second edition of Hitchcock's (1935) *Manual of the Grasses of the United States* have been followed in all matters of nomenclature. The total list of species and varieties encountered in Oklahoma lakes during the investigation was 420. This list included 22 varieties, according to the eighth edition of Gray's *Manual of Botany*. In only one case, however, was a species, and a variety of that species, encountered in the investigation. Because of this, each variety will be considered as a species in the discussion. The formidable table of 420 species has been omitted due to publication costs. However, the complete list of species, with their distribution, will be sent upon request.

The writer wishes to acknowledge the help of Louis Bouchard, Harold Dundee, Gordon Hall, Robert Jenkins, and James Norman in the field investigations. To the field personnel of the U. S. Army Engineers, of the U. S. Fish and Wildlife Service, and of the Oklahoma Game and Fish Department the author expresses his gratitude. The writer is grateful to Dr. G. J. Goodman, Professor U. T. Waterfall, and Ivan Ophel for help in the identification of plants. He is indebted to Mrs. Lovie Whitaker and especially to Dr. R. W. Kelting for help in the preparation of the manuscript.

## TERMINOLOGY

According to Welch (1935) ponds are "very small, very shallow bodies of water in which quiet water and extensive occupancy by higher aquatic plants are common characteristics." "All other bodies of standing water will be referred to as lakes." On the basis of this definition, most of the natural lakes studied (ox-bow lakes and playas) would be classified as ponds. All of the artificial lakes studied, with the possible exception of Crystal Lake, would be considered as lakes under this definition. Because of the difficulties of distinguishing between ponds and lakes on the basis of depth and occupancy by higher plants, the Oklahoma Planning and Resources Board has defined a lake as any water body of 10 acres or more. This basis of separating ponds and lakes has been utilized in the present paper.

With seasonal recession of the waterline in lakes and ponds, the bands of wetland and emergent aquatic plants in these water bodies often are left high and

dry. Since these plants are not in the water, and therefore, not in the lake proper, perhaps they should be excluded from the investigation. The more logical procedure is to include them, even though they may be out of the lake at the time of study. During the second year of the investigation (1949) it was found that the vegetation of the flood zone was very different from that above the uppermost drift line. The phenomenon obviously was due to the destruction of the former vegetation by inundation and the subsequent invasion by weedy plants. In view of this fact, it was decided to include all plants of the flood zone in the investigation. It should be emphasized that this study has included not only the plants in the *lake proper* but also those of the *lake basin,* and thus has comprised many terrestrial species, not ordinarily included in lake investigations.

The classification of marginal plants utilized by Hess and Hall (1945) is used in this paper. Woody plants are divided into intolerant, moderately tolerant, and tolerant species with relation to water levels. The herbaceous plants are divided into terrestrial, wetland, and aquatic species. Of the aquatic species (emergent, floating, submerged) the floating plants are further subdivided into three subgroups: pleustonic species—minute, free-floating plants; floating mat plants—relatively large plants which form mats on the water surface; and floating leaf species—with leaves typically attached to rhizomes in the substratum.

Certain terms in connection with water levels should be defined at this point. Most pools experience a considerable progression (rise) of water level in the spring and a notable recession (drop) in water level during the summer and autumn. The maximum extent of the progression can usually be determined by drift lines and erosion scarps (Figs. 2 and 3). Progression above the usual operating pool level results in a hydroperiod (inundation of soil surface) for plants not normally subjected to flooding. Recession below the summer pool level, on the other hand, produces an aeroperiod (exposure of previously inundated soil surface to air) for plants ordinarily protected by water. Water level management is the scientific use of progression and recession to control plants or mosquitoes or to produce the maximum of aquatic wildlife resources.

FIG. 2. Three drift lines in flood zone of Lake Texoma, Summer, 1948.

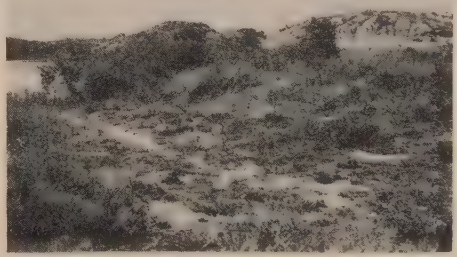

FIG. 3. Flood zone of Fort Supply Reservoir, August, 1949, with erosion scarp (right background).

Since many of the reservoirs are designed for flood control, a zone ten to thirty feet vertically, below the top of the spillway, is reserved for the storage of flood waters. The water level in this flood zone, or flood surcharge zone, is lowered during the winter in anticipation of the spring flood waters. The actual flood zone, in a given year, is the area between the uppermost drift line and the summer pool level. About June 1, the level is allowed to drop to the summer

pool level. This lake level varies about two feet vertically due to relative rates of inflow and outflow, wind direction, wind velocity and height of waves. The water level typically recedes slowly from the summer pool level due to an excess of evaporation over precipitation and to the use of water for various purposes. The area immediately below the summer lake level is known as the recession zone. The recession zone varies greatly in width from season to season, and may be eliminated temporarily by summer floods, but usually attains its greatest area in October. Below the recession zone is the continuous water zone, the area below the minimum water level.

In constant level pools, with an average annual amplitude of water levels of less than two feet, the zones are characterized by general ecological plant types as follows: drift line (terrestrial plants), flood surcharge zone (terrestrial species), summer pool level (wetland plants), recession zone (emergent aquatics) and continuous water zone (floating leaf and submerged aquatics). In recent impoundments with erratic and wide fluctuation of water levels (*e.g.*, Altus, Canton) no wetland fringe becomes established and there is no distinction between the flood zone and the recession zone.

## Description of Lakes

For purposes of discussion the state was divided into four sections as follows: Eastern (94° 30′ W-96° W); Central (96° W-98° W); Western (98° W-100° W; and the Panhandle (100° W-103° W). The water bodies studied in the various sections of the state were as follows: Eastern, four ox-bows and six reservoirs; Central, eight reservoirs; Western, ten reservoirs; Panhandle, four playas (Fig. 1). In the Eastern section, Grand, Spavinaw, Cedar, and Greenleaf Reservoirs occur in limestone basins and are characterized by relatively clear, bluish water. Grand Lake is subject to an annual fluctuation of ten or more feet, but Spavinaw, Cedar, and Greenleaf Reservoirs are essentially constant level lakes. Henryetta and McAlester Reservoirs are shallow water bodies characterized by high turbidity. Curtis Lake, a shallow ox-bow of the Poteau River, and nearly filled with vegetation, is now a part of the Wister Reservoir. Roebuck is a deep ox-bow of the Red River near Hugo, Oklahoma. Clear and Grassy Lakes are shallow, alluviated ox-bows of the Red River, located in the southeastern corner of the state. Both are subject to considerable recession during the growing season and present exposed flats, often 500 or more feet wide, in the recession zone.

In the Central section, no natural lakes were encountered but eight reservoirs were investigated (Fig. 1). Ponca City, Mountain, and Murray Reservoirs occur in limestone areas, but the Shell Reservoir is a sandstone lake. Lakes Hefner, Overholser, and Crystal are situated on Permian redbeds and Lake Texoma extends over several geological formations. Of the above lakes, Ponca City, Hefner, Overholser, and especially Texoma, are known to have wide fluctuation of water levels. Crystal and Mountain Lakes, on the other hand, have little fluctuation and have well developed zonation.

Although there are no natural lakes in the Western section, there is much diversification in the ten reservoirs studied in the area. Salt Plains Reservoir, being impounded on the famous Great Salt Plains, is a brackish water lake. Altus, Canton, and Fort Supply Reservoirs are designed for irrigation or flood control, and have wide amplitude of water levels and very poor zonation of plants. Lake Hobart is a small water supply lake with moderate fluctuation of water level. The Wichita Mountain lakes are located in granitic basins, are essentially constant level pools, are relatively clear, and possess excellent plant zonation.

In the Panhandle no reservoirs were studied but four playas were investigated

in some detail (Fig. 1). A playa is usually defined as a temporary or wet weather lake. In the smaller depressions water may be present for only a few weeks, but in others, water may remain for a period of two or more years. In the Hitchland Playa, for example, the water was about 4 feet deep in the spring of 1949 but had been 9 feet above that level one or two years earlier. When seen in June of 1950, however, a crop of wheat was growing in the bottom of the playa. According to Parker and Whitfield (1945) playas are formed when naturally low spots dry up and the bottom sediments are subjected to wind erosion. They state that the playas are formed by wind action, since the northeastern side of a playa is higher than the southwestern rim, a result of the action of prevailing southwesterly winds.

## Climate

The most important climatic factors in determining the distribution of higher aquatic plants in lakes throughout the state are precipitation, evaporation, wind, and temperature. The average annual precipitation in Oklahoma by sections is approximately as follows: Eastern, 41 inches; Central, 33 inches; Western, 26 inches; and Panhandle, 19 inches. The rate of evaporation varies considerably throughout the state. The total evaporation, in inches, for the seven months growing period (April through October) was as follows for two of our key reservoirs: Grand River Dam (Eastern Section) 1948, 49.71; 1949, 44.73; 1950, 51.00. Fort Supply Dam (Western Section) 1948, 72.17; 1949, 60.61; 1950, 63.74. Presumably the evaporation rate in the Panhandle would be still higher (Weather Bureau 1948, 1949, 1950). According to the precipitation-evaporation index of Thornthwaite (1933) most of our Eastern section is in the humid (forest) zone (with an index of 64-127); the Central section (42-64) and Western section (32-42) are in the subhumid (grassland) province, and the Panhandle (16-31) is in the semiarid (steppe) province. Wind decreases the establishment of aquatic plants by its direct action and by augmenting turbidity, especially in shallow lakes. Temperature is important in limiting the north-south distribution of plants and by attenuating or eradicating aquatic plants on exposed portions of lake basins during the winter.

## Lake Conditions

The conditions for the development of macroscopic plants in lakes may be classified as *physical, chemical,* and *biotic.* Physical factors include amplitude of water levels, turbidity, sedimentation, type of bottom, and depth and temperature of the water. Of the chemical factors, oxygen tension, carbon dioxide, nutrients, acidity, and alkalinity are the factors most investigated. Of the biotic agencies, man is paramount, since he builds and manages reservoirs. Plant competition is important in determining succession and dominance. Animal activities such as the feeding of rough fishes, aquatic mammals, and migratory waterfowl undoubtedly contribute considerably to the development and distribution of the higher aquatic plants.

### *Physical factors*

Amplitude of water levels is the most critical factor in the establishment of vegetation in a given water body. In Oklahoma, lakes and ponds are usually full in the spring but gradually recede from two to four feet by late September (Harper and Stout 1944). If heavy rains occur during the summer, lakes are refilled to the summer pool elevation or even above into the flood surcharge zone. Progression during the growing season, if prolonged, destroys herbaceous and woody terrestrial plants, attenuates or destroys wetland plants and favors landward extension of wetland and aquatic plants. Hall, Penfound, and Hess (1946) concluded that "continuous flooding dur-

ing the growing season affected all woody species adversely." Featherly (1940) found that Kentucky coffee tree, bur oak, green ash, cottonwood, hackberry, and honey locust did not survive fifteen months of flooding to a depth of several feet in Lake Carl Blackwell, in north central Oklahoma. In the present investigation, the most striking example of "drowning" of woody plants was the destruction of nearly all of the *Populus deltoides,* up to 35 feet tall, *Salix interior, Salix nigra,* and *Tamarix gallica* plants in the Fort Supply Reservoir by retained flood water in the summer of 1951. Our observations in Oklahoma indicate that the only woody plants that have survived near the summer pool level are moderately tolerant or tolerant species. It has also been observed that silt and water, in combination, are more effective in destroying woody species than water alone.

Recession below the summer pool level is possibly even more important than progression in determining the plant population of lakes and ponds. In a relatively constant pool, a narrow fringe of wetland plants occurs in the environs of the summer pool level, and emergent, floating leaf, and submerged aquatic plants occur as belts in progressively deeper water. When recession occurs, the various zones, from the summer pool level lakeward, are exposed to the air. If recession is considerable and the aeroperiod is prolonged, the emergent, floating leaf and even the submerged aquatics are destroyed and a new bare area is available for the ecesis of terrestrial and wetland plants.

The lakes of the prairies and plains "are subject to much greater wind action than the lakes of hilly or wooded areas. Since they are usually shallow, the resulting wave action stirs up the bottom, resultng in increased turbidity" (Jewell 1927). Turbidities of prairie lakes and ponds may range up to 300 parts per million in the spring but are relatively low in the summer and autumn. In Oklahoma, "Impoundments were found to be clear when: (1) large areas of their basins support good growths of submerged higher aquatic plants; (2) sufficient organic matter is carried into them from the watershed; (3) organic matter or commercial fertilizers have been added to the water" (Irwin 1945). It is believed by Irwin that "materials which release positive ions decrease turbidity by precipitating soil particles." Turbidity is also caused by leachates of decaying plant parts, and by some industrial wastes, but erosion materials appear to be the important turbidity-producing substances in Oklahoma.

"Sedimentation enters into the development of lakes and determines the soils, the color of the water, the abundance of the electrolytes, the hydrogen-ion concentration, and the quality and quantity of the vegetation in them" (Wilson 1939). He might have added that it also determines the longevity of lakes. The average maximum suspended matter carried by Oklahoma rivers in flood is about 1.0 per cent (Harper and Murphy 1930). In a study of Boomer Lake, McCormack (1930) found that silting took place at the rate of about 9 inches per year, which would indicate an effective live of 25 years for the reservoir. The annual rates of silting for six Oklahoma lakes, in per cent of total capacity, from 1934 to 1938 were as follows: Spavinaw, 0.34; Ardmore Club, 0.55; Boomer, 0.59; Sapulpa, 0.74; Guthrie, 1.03; and Clinton, 1.03 (Eakin and Brown 1939). Since muddy waters concentrate near the base of the dams (with clear water on top), it is suggested that an important reduction of the rate of silting might be attained by the discharge of these mud-laden waters by gates near the base of the dam (Eakin and Brown 1939). From these few data, and from talks with many men interested in lake biology, it is obvious that sedimentation of Oklahoma lakes is very great and that many of the reservoirs, particularly in the prairies and

plains, have a very short life expectancy.

The type of bottom is very important in the ecesis of lake plants. The poorest growth occurs on nearly pure sand, gravel or rock, whereas the best growth is upon ogranic muds, or upon soft, silty, or clayey inorganic muds. Apparently all of the above bottom types are present in the lakes of Oklahoma.

Depth of water is exceedingly important, especially in the relatively turbid lakes that occur in Oklahoma. In general, emergent aquatic plants extend to depths of 6 feet, floating leaf aquatics reach depths only a little greater, 8.5 feet, but submerged plants may occur in water 20 feet deep. Coontail (*Ceratophyllum demersum*) has been observed at a depth of 29 feet at Wakulla Springs, Florida (Martin and Uhler 1939). The stoneworts (*Characeae*) may ecize in water as much as 40 feet in depth (Welch 1935). In Oklahoma, the average maximum depths (in feet) attained by some of the aquatics were as follows: *Typha domingensis,* 2.2; *Justicia americana,* 3.8; *Potamogeton nodosus,* 4.2; *Heteranthera dubia,* 4.2; and *Ceratophyllum demersum,* 8.0. These limited measurements suggest that average maximum depths in Oklahoma lakes are much lower than the average maxima usually quoted.

"The effect of moderately low temperatures upon rooted aquatics does not appear to be one of the very important ecological factors in their ultimate growth and distribution" (Wilson 1939). It should be pointed out, however, that in Oklahoma, the southern lakes possess a considerably different flora than the more northern lakes, presumably due to the limiting effects of temperature on the north-south distribution of plants. It is probable also that winter temperatures are effective in attenuating or destroying submerged and even floating leaf and emergent aquatic plants on portions of lake basins exposed by notable recession.

*Chemical factors*

The chemical factors typically investigated by limnologists are oxygen, carbon dioxide, nutrients, acidity and alkalinity. Wood (1952) found a marked correlation between species occurrence of the Characeae and salinity, methyl orange alkalinity and *pH* values. Although plants modify the oxygen tension of aquatic habitats very greatly, it is probable that oxygen tension is not a limiting factor in the distribution of higher aquatic plants throughout the lakes of Oklahoma. However, oxygen tension may be a potent factor in succession since floating plants, especially pleustonic and floating mat species, may reduce the oxygen tension to as low as 0.1 part per million. It is probable that carbon dioxide and nutrients are not important factors in the distribution of rooted aquatic plants in Oklahoma lakes.

"In various kinds of natural, unmodified waters, hydrogen-ion concentration differs from at least *pH* 3.2 to 10.5 inclusive" (Welch 1935). In Oklahoma lakes, away from communities of aquatic plants, and at a depth of one meter, the typical *pH* range was from 7.0 to 8.6. The lowest *pH* figures were obtained from lakes in granite basins whereas the highest figures were procured in the Salt Plains Reservoir.[2] The abundance of hydrophytes in Oklahoma waters parallels the results of a study of the vegetation of 102 lakes in northern Wisconsin which showed that aquatic plants were most numerous in circumneutral lakes (Wilson 1939).

Alkalinity is often a potent factor in determining the species of plants that can survive in a given lake. Alkaline lakes, typically with a *pH* of 8.0 to 8.6 are present in the Western and Panhandle sections of the state. Salt Plains Reservoir is an alkaline water lake with a chloride content of 461 to 1728 parts per million

[2] Personal communication with Dr. Howard Clemens, Department of Zoological Sciences, University of Oklahoma.

(Jenkins 1949). Except in the fresh water arm of the Salt Plains Reservoir, the vegetation includes such salt-tolerant dominants as *Distichlis stricta, Scirpus americanus, S. paludosus, Sesuvium verrucosum, Sporobolus airoides,* and *Tamarix gallica.*

*Biotic factors*

Of the biotic factors, man is by far the most important. In the history of Oklahoma, he has been the maker and the victim of tremendous erosion which has scarred the hillsides and filled streams and lakes with silt. In recent years, he has attempted to correct these conditions by contour farming, grassland agriculture, and by the construction of many impoundments. Except for upstream protection, reservoirs have been the object of reasonable management, but farm ponds have received little attention, rarely being properly sodded or protected from unrestricted grazing (Kelting and Penfound 1950). On small reservoirs, and in ponds generally, grazing animals constitute a major factor in limiting the establishment of wetland and emergent aquatic plants.

Of the feral animals, the beaver modifies the habitat by impounding water, which in turn kills many herbs and trees due to an increase in the water level. Muskrats feed on rhizomes of marsh plants and often create local areas free of marsh vegetation. Rough fishes increase turbidity and limit the establishment of submerged and floating leaf aquatic plants. Apparently the most important role played by birds is in the distribution of fruits and seeds, usually in mud on their beaks and feet. Duckweeds often adhere to the feathers of ducks and may be transported in this way (Arber 1920). The internal dissemination of seeds of hydrophytes by birds was proved by Guppy (1893) who dissected many aquatic birds, and found that the many seeds therein germinated better than seeds which had not been ingested.

## Plant Communities

*General facts*

Southeastern forest types listed by Putnam (1951) that occur in the bottomlands of Oklahoma, along the edges of sloughs, ponds, and lakes, are cypress, cottonwood-willow, overcup oak-bitter pecan, and hackberry-elm-ash. Little and Olmsted (1931) list the following zonation for lakes of eastern Oklahoma: *Nymphaea* → *Zizaniopsis* → *Alnus-Cephalanthus* → *Taxodium* → *Liquidambar-Nyssa.* It should be noted that the *Taxodium* zone occurs above the *Alnus-Cephalanthus* belt. For Muskogee County, the common succession (zonation) of ponds include *Jussiaea* → *Eleocharis-Juncus* → *Bidens-Boltonia* → *Populus-Salix* (Little 1938). Little noted that the ponds of Muskogee County did not have a well-developed aquatic vegetation and were especially poor in aquatic seed plants.

According to Parker and Whitfield (1945), *Buchloe dactyloides, Eleocharis macrostachya, Euphorbia marginata,* and *Franseria tomentosa* were the predominant species in the playas of the Oklahoma Panhandle. Reed (1930) in a study of the playas of the Staked Plains of western Texas, listed *Franseria tomentosa, Heteranthera limosa, Myosurus minimus, Marsilea vestita, Polygonum camporum,* and *P. pennsylvanicum* as important hydrophytes. He also listed border plants, many of which were found nowhere else in the region. *Buchloe dactyloides* (a terrestrial plant) was found to resume normal growth after being "submerged for a period of over 14 months" in playas (Porterfield 1945).

After a reservoir is drained, a remarkable assemblage of plants appears on the lake bottom. St. John's Pond, Long Island, New York, was drained for the first time in 70 years in the spring of 1904. By late summer, 140 species of flowering plants were counted (Shull 1914). In explanation, he stated that "the great majority of the species, however, were an-

nuals and must have developed from seeds lying in the mud." Similar observations were made at Cranbrook Lake, Michigan, by Billington (1938) who believed that the seeds had remained dormant on the bottom for approximately twenty-five years. More recently (1946-47) Lake Tonganoxie, Kansas, was drained and 93 species were collected from the lake bottom. *Polygonum lapathifolium* composed about 90 per cent of the total cover (McGregor 1948). As far as is known, no comparable list has been made for any lake in Oklahoma. It is probable that a fairly similar situation exists in the recession zone of Oklahoma lakes since the plant lists from these zones are similar to the list compiled by McGregor.

The typical zonation of plants is the same for natural and artificial ponds and lakes, provided they are accorded the same treatment. The drift lines and the flood zones are usually occupied by terrestrial communities; the summer pool level is characterized by wetland communities; the recession zone is occupied mostly by emergent aggregations and the continuous water area is occupied by floating leaf and submerged aquatic communities (Figs. 4, 5, and 6). If the aquatic communities are destroyed by an extended aeroperiod, their place is immediately taken by one or more terrestrial or wetland communities. If all except the emergent aquatics are destroyed, the new zonation (from the land lakeward) is as follows: terrestrial → wetland fringe → emergent aquatics → terrestrial → wetland communities. An inverted zonation is thus produced, with terrestrial and wetland plants below the wetland fringe and the emergent aquatics.

FIG. 4. *Erigeron canadensis, Euphorbia-Lippia,* and *Euphorbia marginata* communities (left to right) at Hitchland Playa, October, 1949.

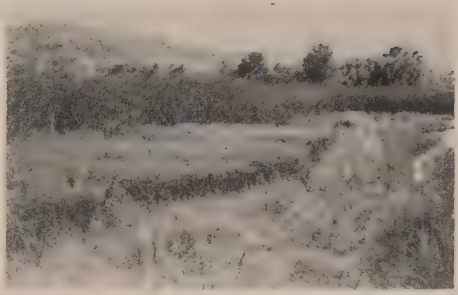

FIG. 5. *Coreopsis tinctoria, Juncus nodatus,* and *Typha domingensis* communities (right to left) at Rush Lake, July, 1949. Open water (left).

FIG. 6. *Potamogeton nodosus* (foreground), and *Typha domingensis* (right) communities at Elmer Thomas Lake, Summer, 1948.

A total of 48 plant communities was encountered in the Oklahoma lakes investigated. Only 6 woody aggregations were encountered and none of these was observed in playas of the Panhandle (Table I). Salt water communities were limited to the Salt Plains Reservoir in the Western section. Fresh water herbaceous communities were about equally distributed between the various sections. There were fewer terrestrial (13) or wetland (15) than aquatic (20) aggregations (Table I). However, there were fewer aquatic communities (3) in the Pan-

TABLE I. *Plant communities of Oklahoma lakes*

*Type: T, terrestrial; W, wetland; Aq, aquatic. Sections: E, eastern; C, central; W, western; P, panhandle. No., number of lakes in which a given community occurs.*

| | Type | E | C | W | P | No. |
|---|---|---|---|---|---|---|
| **Woody communities** | | | | | | |
| Flood zone (terrestrial) | | | | | | |
| *Fraxinus-Ulmus* | T | X | X | | | 4 |
| *Prunus-Rhus* | T | | | X | | 1 |
| *Smilax bona-nox* | T | | X | | | 1 |
| Summer pool level (wetland) | | | | | | |
| *Alnus serrulata* | W | X | | | | 1 |
| *Populus deltoides* | W | X | X | X | | 6 |
| *Salix-Tamcriz* | W | X | X | X | | 22 |
| **Fresh water herbaceous communities** | | | | | | |
| Drift lines | | | | | | |
| *Andropogon hallii* | T | | | X | | 1 |
| *Lythrum-Verbena* | T | | | | X | 2 |
| Flood zone | | | | | | |
| Residual | | | | | | |
| *Andropogon virginicus* | T | X | | | | 1 |
| *Buchloe dactyloides* | T | | | | X | 1 |
| *Cynodon dactylon* | T | | X | X | | 2 |
| *Panicum-Paspalum* | T | X | | | | 1 |
| *Panicum-Sporobolus* | T | | X | | | 2 |
| Flood-induced | | | | | | |
| *Ambrosia-Gutierrezia* | T | | X | | | 1 |
| *Coreopsis tinctoria* | W | | X | X | | 4 |
| *Echinodorus rostratus* | Aq | | | | X | 1 |
| †*Erigeron canadensis* | T | | X | X | X | 5 |
| *Euphorbia-Lippia* | W | | | | X | 1 |
| †*Ephemeral weed* | TW | X | X | X | X | 12 |
| Summer pool level zone | | | | | | |
| *Carex aquatilis* | W | | X | | | 1 |
| *Cyperus ferruginescens* | W | | X | | | 1 |
| †*Eleocharis macrostachya* | Aq | | X | X | X | 6 |
| *Panicum agrostoides* | W | X | X | | | 4 |
| Recession zone | | | | | | |
| Aeroperiod a month or more | | | | | | |
| **Acnida-Aster* | W | X | X | X | X | 9 |
| *Chenopodium-Myosurus* | W | | | | X | 1 |
| *Franseria-Xanthium* | W | | | | X | 2 |
| *Polygonum persicaria* | W | | | | X | 2 |
| *Sida-Triticum* | T | | | | X | 1 |
| Aeroperiod short or none | | | | | | |
| *Eleocharis quandrangulata* | Aq | | X | X | | 3 |
| *Juncus nodatus* | Aq | X | | X | | 5 |
| *Justicia americana* | Aq | X | X | X | | 10 |
| *Leersia-Saururus* | Aq | X | X | X | | 6 |
| *†*Polygonum coccineum* | Aq | X | X | | | 2 |
| *†*Polygonum lapathifolium* | Aq | X | X | X | | 7 |
| *Typha domingensis* | Aq | X | X | X | | 10 |
| *Zizaniopsis miliacea* | Aq | X | | | | 3 |
| Continuous water zone | | | | | | |
| Pleuston | | | | | | |
| *Lemna-Spirodela* | Aq | X | X | | | 1 |
| Floating leaf | | | | | | |
| *Nelumbo lutea* | Aq | | X | X | | 3 |
| *Nuphar-Nymphaea* | Aq | X | | | | 2 |
| Floating mat | | | | | | |
| †*Jussiaea repens* | Aq | X | X | | | 2 |
| Submerged | | | | | | |
| *Cabomba caroliniana* | Aq | X | | | | 1 |
| *Ceratophyllum demersum* | Aq | X | X | X | | 5 |
| *Chara contraria* | Aq | X | X | X | X | 5 |
| *Heteranthera dubia* | Aq | X | | | | 1 |
| *Potamogeton nodosus* | Aq | X | X | X | | 9 |
| *Potamogeton pectinatus* | Aq | | | X | | 1 |
| **Salt water communities** | | | | | | |
| Flood zone | | | | | | |
| *Distichlis stricta* | W | | | X | | 1 |
| Summer pool level | | | | | | |
| *Scirpus americanus* | W | | | X | | 2 |
| *Scirpus paludosus* | W | | | X | | 1 |

*present also in flood zone; †present also in recession zone.

handle than in the other sections (Eastern, 15; Central, 12; Western, 12).

*Woody plant communities*

Only six woody aggregations were encountered in Oklahoma lakes. Wherever woody communities occur, each one may shade out and substitute for two, or even more, herbaceous communities. The woody plant communities of the flood surcharge zone include one arborescent and two frutescent aggregations (Table I). The *Fraxinus-Ulmus* associes occurs in four lakes of the Eastern and Central sections. Although *Celtis laevigata* and *Ulmus americana* are codominants throughout the area, only *Diospyros virginiana* and *Fraxinus pennsylvanica subintegerrima* are present in the flood zones of reservoirs. These species are so tolerant of flooding during the growing season that they often occur in considerable numbers in the next two lower (*Populus deltoides, Salix-Tamarix*) communities. The *Prunus-Rhus* associes was observed only in the flood zone of Fort Supply Reservoir in the Western section. Many specimens of both dominants, *Prunus augustifolia* and *Rhus aromatica serotina,* had been destroyed by retained flood water by 1950, and many weedy species, particularly *Euphorbia missurica intermedia,* had invaded the area (Fig. 3). Retention of flood water during the summer of 1951 destroyed nearly all the remaining woody plants. At present, therefore, this woody aggregation does not occur in any of the Oklahoma lakes studied. An unusual frutescent community of the flood zone is the *Smilax bona-nox* consocies. It was reported by Dr. E. L. Rice in flooded portions of grazed pastures in the vicinity of the University of Oklahoma Biological Station on Lake Texoma. It consists mainly of the spinescent *Smilax bona-nox,* which tolerates heavy grazing pressure, and the unarmed *Ampelopsis arborea,* which develops under the protection of the dominant species.

The woody plant aggregations at the summer pool level include *Alnus serrulata, Populus deltoides,* and *Salix-Tamarix* communities. The *Alnus serrulata* consocies occurs only on one lake (Cedar) in the Eastern section. The *Populus deltoides* consocies occurs in seven lakes in Central and Western Oklahoma (Table I). It develops in the upper portions of the summer pool level zone and, in some lakes, extends well up into the flood zone. Usual components include *Platanus occidentalis* (Central section), *Populus deltoides, Populus sargentii* (Western section), and *Salix nigra.* Although *Populus deltoides* and *Salix nigra* often occur together, the former usually occupies somewhat higher ground.

The *Salix-Tamarix* associes is the most widespread of any of the plant communities found in Oklahoma lakes (Table I). It has been observed in 22 lakes and in all four sections of the state, although the stand in the Panhandle section at Lake Tucker near Kenton was not investigated. This associes comprises *Cephalanthus occidentalis, Forestiera acuminata* (Eastern section), *Populus deltoides, P. sargentii* (Western section), *Salix amygdaloides* (Eastern section), *S. interior, S. nigra,* and *Tamarix gallica* as dominants (Figs. 5 and 6). All of the above species have been observed in pure stands, but all combinations (except as precluded by geographic distribution) of species may occur. In view of the lower elevation at which this aggregation occurs and its much wider distribution than the *Populus deltoides* consocies, it is felt that the inclusion of the dominants of *Populus deltoides* and *Salix-Tamarix* aggregations into one community (*Populus-Salix*) is not desirable.

*Herbaceous communities*

*1. Drift lines*

Aggregations of plants often become established on drift lines, especially at the uppermost edge of the flood zone. These populations are not significantly different from other weedy aggregations of the

flood zone in the Eastern and Central sections. However, in the Western and Panhandle sections where soil water is often deficient, the drift not only destroys the original dominants but also increases the water content of the soil sufficiently to allow for the development of species very different from the remainder of the flood zone. In 1949, a consocies of *Andropogon hallii,* with *Cenchrus pauciflorus* as the most abundant secondary species, became established high on the limestone riprap of the Fort Supply dam. It is doubtful, however, that this community will survive the xeric conditions of the habitat or the periodic extreme inundations that occur during the growing season. In the Panhandle section, a *Lythrum-Verbena* associes occurred on drift lines at Gate and Hitchland Playas. The dominants were *Lythrum alatum* and *Verbena bracteosa* at Gate Playa and *Ambrosia psilostachya, Helianthus petiolaris,* and *Verbena bracteosa* at the Hitchland Playa. Other drift line communities, especially at Lake Altus, were observed but not studied.

### 2. Flood zone

*Residual.*—Several residual herbaceous aggregations were encountered in the flood surcharge zone during the investigation (Table I). These communities are the result of survival of original grassland components following prolonged progression above the summer pool level. *Andropogon virginicus* (Eastern section) survives flooding fairly well and often occurs in nearly pure stand, especially in portions of revegetating, abandoned fields that occur in the flood zone. In the Western section, and especially in the Panhandle, *Buchloe dactyloides* often survives in flood zones after its companion species have been destroyed by flood waters. At Hitchland Playa a heavy sod of *Buchloe dactyloides* was present four feet vertically below the uppermost drift line and fragments occurred down to a point over seven feet vertically below the highest flood waters (Fig. 4). *Cynodon dactylon* is another water tolerant species which forms nearly pure communities in flood zones. Excellent examples can be seen at Lake Texoma and Salt Plains Reservoir. Another residual community is the *Panicum-Paspalum* associes near the dam at Wister Reservoir. It consists largely of *Panicum helleri* and *Paspalum circulare.* One that is widespread in the prairie lakes of the Central section is the *Panicum-Sporobolus* associes. This community becomes established just above the summer pool level. It comprises *Panicum virgatum* and *Sporobolus asper* as dominants with *Aster exilis* and *Coreopsis tinctoria* as common companion species.

*Flood-induced.* — Flood-induced communities are formed in the flood surcharge zone, and also in the recession zone, when most of the former plants growing in the area are destroyed by inundation. These new communities are always composed of weedy species which are able to ecize on the bare areas produced (Figs. 2, 3, and 4). In the spring and summer, a population of ephemeral weeds develops, flowers, fruits and disappears in a few weeks. This group of plants is followed by another group of species which flowers and fruits during the autumn. The ephemeral (spring-summer) weed population probably consists of several plant communities, based on distribution and elevation, but is here treated as a single community. Predominant species include the following: *Amaranthus albus, *Ammannia coccinea, Bacopa rotundifolia, Conobaea multifida, Cyperus inflexus, Diodia virginiana, Eclipta alba, Eleocharis obtusa, Fimbristylis autumnalis mucronulata, *Hemicarpha drummondii, Lepidium densiflorum, *Lindernia dubia, *Mollugo verticillata, *Myosurus minimus, *Rorippa obtusa, R. sessiliflora, Rotala ramosior, *Sida hederacea, Spermacoce glabra,* and *Veronica peregrina.* Certain of the above species occurred in the Eastern section only; others were encountered only

in the Panhandle and only *Veronica peregrina* was encountered in all four sections of the state. The more important species are marked with an asterisk.

The autumnal species which become established in the ephemeral weed population include *Acnida tamariscina, Ambrosia psilostachya, Aster exilis, Coreopsis tinctoria, Euphorbia marginata, Erigeron canadensis, Franseria tomentosa, Gutierrezia dracunculoides, Haplopappus ciliatus,* and *Xanthium italicum.* After the maturation of the ephemeral weeds, *Erigeron canadensis* often gained complete dominance and sometimes occurred in nearly pure stands up to eight feet tall (Fig. 4). This community was encountered in five reservoirs in the Central, Western, and Panhandle sections. Common associates included *Coreopsis tinctoria, Euphorbia marginata, Gutierrezia dracunculoides, Rumex crispus,* and *Xanthium italicum.* Another autumnal weedy aggregation is the *Ambrosia-Gutierrezia* associes which was observed only on Lake Texoma. *Ambrosia psilostachya, Gutierrizia dracunculoides,* and residual *Panicum virgatum* formed a distinctive community to a point eight feet above the summer pool level. Another segregate is the *Coreopsis tinctoria* consocies, found in four reservoirs in the Central section (Fig. 5). *Aster exilis, Juncus torreyi, Lippia lanceolata,* and *Paspalum distichum* are common associates. The *Echinodorus rostratus* aggregation was observed only once, in Gate Playa, on August 16, 1949. This aquatic community had become established during the wet summer of 1949 above the summer pool level in 0.3 feet to 1.0 feet of water. It was not present in Gate Playa in 1950 nor was it ever observed in any of the other playas during the course of the investigation. This phenomenon is typical of the ephemeral nature of many plant communities in ponds and lakes with a wide amplitude of water level. The *Euphorbia-Lippia* associes was encountered only once, in the Hitchland Playa of the Panhandle section (Figure 4). *Buchloe dactyloides* (not destroyed by flooding), *Euphorbia marginata,* and *Lippia cuneifolia* were the widespread dominant species although *Actinea odorata, Oenothera canescens,* and *Sophora sericea* were abundant locally.

### *3. Summer pool level zone*

The herbaceous, wetland communities in the summer pool level zone (about three feet vertically) were most numerous in the Central section (Table I). As a general rule, the wetland aggregations of this zone were much narrower and more manifest than other communities. This was especially true for the *Carex aquatilis, Cyperus ferruginescens,* and *Panicum agrostoides* consocies. The *Carex aquatilis* and *Cyperus ferruginescens* communities consisted of one dominant each, and were encountered in only one reservoir each, the former at Lake Overholser and the latter at Lake Hefner. The *Eleocharis macrostachya* aggregation was observed in six reservoirs in the Central, Western, and Panhandle sections. It migrates often into the recession zone whenever wide recession occurs during the early part of the growing season. Although *Eleocharis macrostachya* often occurs in pure stand, *Echinochloa crus-galli, Ludwigia palustris,* and *Paspalum distichum* are common secondary species. *Polygonum persicaria* is a predominant species in Gate and Hitchland Playas. The *Panicum agrostoides* consocies is a relatively narrow distinctive community occurring primarily in the Eastern section.

### *4. Recession zone*

*Aeroperiod a month or more.*—If recession below the summer pool level is considerable and of long duration, many of the aquatic plants are destroyed and weedy terrestrial and wetland species become established below the wetland fringe. Ephemeral weed communities and the

*Erigeron canadensis* consocies of the flood zone, especially, may occur in the exposed area of the recession zone. In addition, several other communities are characteristic of this area (Table I). The *Acnida-Aster* associes is an autumnal weed community of this zone, which was observed in nine reservoirs, and in all sections of the state. This community, also present in the flood zone, is dominated by *Acnida tamariscina* and *Aster exilis*. The other four communities are characteristic of playas (Table I). The *Chenopodium-Myosurus* associes was encountered only once, in the Gate Playa in June, 1950, following recession due to a very dry spring season. The dominants consisted primarily of *Chenopodium incanum, Erigeron canadensis,* and *Myosurus minimus*. Prominent secondary species were *Atriplex argentea, Aster exilis,* and *Monolepis nuttalliana*. At a somewhat lower level in Gate Playa, at the same time, the *Franseria-Xanthium* associes was encountered. The same community occurred in the Griggs Playa. Dominants included *Eleocharis macrostachya, Franseria tomentosa, Helianthus ciliaris* (Griggs Playa only), and *Xanthium italicum*. The *Polygonum persicaria* consocies was encountered in the Griggs and Hitchland Playas. The major dominant was *Polygonum persicaria* with *Eleocharis macrostachya* and *Polygonum ramosissimum* as common secondary species. The big surprise during the study of the playas was the discovery of a wheat crop in the bottom of the Hitchland Playa in an area that contained approximately thirteen feet of water some two years earlier. Since the only important weed was *Sida hederacea,* this ephemeral community has been called the *Sida-Triticum* associes.

*Aeroperiod short or none.*—Emergent, aquatic communities occur lakeward from the summer pool level to a depth of about four feet provided recession is slight or of short duration (Figs. 5 and 6). Of the eight communities, the *Justicia americana* and *Typha domingensis* consocies were the most numerous, each occurring in ten lakes (Table I). The emergent aquatic communities studied usually consisted of a single dominant, usually without secondary species. However, the *Eleocharis quadrangulata* consocies comprised *Eleocharis quadrangulata crassior* as the major dominant, with *Eleocharis macrostachya, Juncus nodatus,* or *Scirpus validus* as prominent secondary species in certain reservoirs. Dominants of the *Leersia-Saururus* associes included *Leersia oryzoides,* which often forms pure stands in seepage areas, *Polygonum hydropiperiodes,* and *Saururus cernuus*. The *Typha domingensis* consocies sometimes includes *Typha latifolia* as a codominant (Murray, Overholser, Spavinaw Reservoirs) but usually occurs in nearly pure stand (Figs. 5 and 6). With relation to water depth, the communities were disposed as follows: *Eleocharis quadrangulata, Juncus nodatus,* and *Leersia-Saururus* are found in shallow water; *Typha domingensis* occurs in water of intermediate depth (average maximum, 2.2 feet) whereas *Justicia americana* and *Zizaniopsis miliacea* extend into fairly deep water (average maximum, 3.8 feet). *Polygonum coccineum* and *P. lapathifolium* consocies have been encountered in water at least ten feet deep and yet the dominants flower and set seed when stranded by recession in either the flood or recession zones.

*5. Continuous water zone*

*Pleuston.*—The only pleustonic plant community was the *Lemna-Spirodela* associes, observed at Grassy lake in the Eastern section. The dominants were *Lemna minor* and *Spirodela polyrhiza*. Considerable *Azolla caroliniana* was stranded on the mud in the lower part of the recession zone and may have been an important community component in the spring season.

*Floating leaf.*—Floating leaf aquatic communities are not numerous in Okla-

homa lakes. The *Nelumbo lutea* consocies was studied in three reservoirs in the Central and Western sections but was observed also in ponds in the Eastern section. Although *Nelumbo lutea* was the sole dominant, an understory of submerged plants (particularly *Ceratophyllum demersum*) was usually present. The *Nuphar-Nymphaea* associes was encountered only twice, once in an alluviated ox-bow (Curtis) lake in the Eastern section and in Crystal Lake (planted) in the Central section. Since Curtis Lake is now completely inundated by waters of the Wister Reservoir, it is assumed that the *Nuphar-Nymphaea* associes there has been eliminated. Although *Nuphar advena* occurs in slightly shallower water than *Nymphaea odorata* and may occur separately in pure stand, they are considered as members of the same community.

*Floating mat.*—The only floating mat community observed in Oklahoma lakes was the *Jussiaea repens* consocies. A fragmentary sample, in the floating condition, was encountered in Lake Hefner, in the Central section. The only species in this sample was *Jussiaea repens glabrescens.* An extensive example, stranded and rooted in the recession zone, was encountered in a pastured portion of Grassy Lake in the Eastern section.

*Submerged.*—The submerged aquatic aggregations were fairly numerous in the Eastern section but decreased westward (Table I). The *Cabomba caroliniana* and *Heteranthera dubia* aggregations were encountered only in the Eastern section. The *Ceratophyllum demersum* and *Chara contraria* consocies were widespread and fairly numerous (5 lakes each). The *Chara contraria* aggregation sometimes included *Chara haitensis,* although each often occurred in pure stand. By far the most important submerged community was the *Potamogeton nodosus* consocies (Fig. 6). *Potamogeton nodosus* is a species in which the number of submerged leaves is considerably greater than the number of floating leaves. Since the floating leaves exhibit relatively low cover as compared to typical floating leaf species (*Nelumbo, Nuphar, Nymphaea*), the *Potamogeton nodosus* consocies has been treated as a submerged community. The remaining community (*Potamogeton pectinatus*) was encountered only once, in a protected inlet of the Salt Plains Reservoir in 1948.

### *Salt water communities*

Communities of salt water plants have been observed only in the Great Salt Plains area. The Salt Plains Reservoir has been impounded on the Great Salt Plains, characterized by gleaming white salt flats with elevations around the edges. On hummocks and other elevations (not over four feet high), *Sporobolus airoides* covered the tops and sides except for a consocies of *Distichlis stricta* near the junction of the elevations with the salt flats. *Sesuvium verrucosum* is abundant throughout both communities and forms a pioneer consocies on the salt flat itself. All three communities still exist within the Salt Plains Reservoir, but the *Distichlis stricta* consocies is much the more extensive. In the upper portion of the summer pool level zone of the lake proper, *Scirpus americanus* forms an open community whereas *Scirpus paludosus* forms dense stands at a somewhat lower elevation. The latter community is seen at its best development, however, in the brackish ponds in the sandhills in the vicinity of, but beyond the confines of, the Salt Plains Reservoir.

## Plant Succession

Excellent zonation and succession are characteristic of constant level pools whereas these phenomena are inconstant and negligible in lakes with a wide amplitude of water levels. Let us assume a constant level lake, with fairly rapid sedimentation, a sloping shoreline, and a maximum depth (offshore) where submerged plants cannot become established.

The growth of submerged aquatics "is limited, on the one hand, by light penetration of the water and, on the other, by a zone of floating-leaved species. These latter (water lilies, etc.) exclude submerged species by shading but cannot move into the zone of the submerged forms until the bottom is built up or the water level falls. In still shallower water, emergent species predominate" (Oosting 1948). When filling is sufficient, wetland herbs, shrubs, and trees are able to ecize. Although sedimentation is the major factor in building up the bottom, the aquatic plants aid in raising the soil level by decreasing the flow of water and by contributing raw organic matter to the substratum. The end result is that the various zones move lakeward as the substratum is elevated. Succession is thus accomplished both by the external factor of sedimentation and by the reactions of the plants. Presumably sedimentation would be the predominant factor in lakes of high turbidity whereas plants would be more important in relatively clear lakes.

In lakes with wide fluctuation of water levels, very little plant succession is possible. If progression occurs during the growing season, when the plants are in full verdure, most of the plants in the flood zone are destroyed and a secondary bare area is created. As long as the water remains in the flood zone very little ecesis of aquatic plants can be accomplished below the summer pool level (wetland fringe) because of low light intensity in the relatively turbid water. Many of the wetland and aquatic plants are also destroyed when their leaves are covered with turpid water for a considerable period. This happened to the lotus, *Nelumbo lutea,* in the Wheeler Reservoir, near Decatur, Alabama, when "colonies of lotus were submerged under two to four feet of turbid water for several days." "Flood waters destroyed the leaves and many of the rhizomes of the lotus, but the remaining rhizomes produced a few small leaves of the floating type." (Hall and Penfound 1944).

In the average year in Oklahoma, a vertical recession of 3 to 8 feet below the summer pool level occurs in flood control lakes and playas. This annual recession prevents the ecesis of the emergent, floating leaf, and submerged aquatics that normally populate this area. The exposed area, however, is invaded immediately by terrestrial and wetland plants. Unfortunately, the progression during the next period of high water destroyed these plants and effective succession is prevented. It is thus clear that plant succession and good zonation are impossible in flood control reservoirs, playas, and other water bodies with wide amplitude of water levels.

## Species in Oklahoma Lakes

Of the total list of species and varieties encountered in Oklahoma lakes during the investigation, 182 each were terrestrial and wetland plants and only 56 were aquatic species. The relative abundance of terrestrial plants and comparative paucity of aquatics was due to the wide amplitude of water levels in many natural lakes and reservoirs. However, the per cent of aquatics relative to the total lake population was greater for natural lakes (27%) than it was for the artificial lakes (7%).

The total number of species was about equal in Eastern, Central, and Western sections but was relatively low in the Panhandle. This paucity of species was undoubtedly due to the fact that we sampled only one type of water body (playa) and only four of these. Based on the percentage of the total number of species of each habitat type, there was a gradual decrease in the Panhandle from terrestrial (23) through wetland (17) to the aquatic species (12). The last group was represented by very few individuals, a further indication of the unfavorable conditions for aquatic plants that obtain in the playas.

On the basis of perennation, there were 33 woody plants, 163 annual herbs, and 224 perennial herbs. The last group included four biennials and four species which were either biennials or perennials. Woody species were distributed throughout the sections of the state as follows: Eastern, 26; Central, 23; Western, 16; and Panhandle, 3. As might be expected, the numbers of woody species decreased westward, especially between the Western and Panhandle sections.

There is a remarkable diversity in the distribution of Oklahoma lake plants. In the Eastern section 210 species of plants were sampled in our survey and yet only 12 of these were encountered in the Panhandle section. These species were: *Aster exilis, Echinochloa crusgalli, Eleocharis macrostachya, Erigeron canadensis, Heteranthera limosa, Polygonum coccineum pratincola, P. lapathifolium, P. pennsylvanicum, Sagittaria latifolia, Salix interior, S. nigra,* and *Xanthium italicum.* Of the above species only *Echinochloa crusgalli, Erigeron canadensis,* and *Salix interior* were abundant in each section. Of the 40 aquatic species encountered in the Eastern section only 6 were observed in the Panhandle. That the percentage of aquatic species was not greater was due to the great amplitude of water levels in the playas.

A general comparison of the list of plants in this study with the larger aquatic plants of Oklahoma by de Gruchy (1938) may be of some interest. In his investigation he listed 45 wetland and 74 aquatic species. Although more wetland plants (182) were observed in the present survey, only 56 species of aquatic plants were encountered. De Gruchy included 36 aquatics not listed in the present survey and we have observed 18 aquatic species not listed by him. During the present survey, more aquatics were observed in borrow pits, ditches, ponds, seeps, springs, and streams than in the lakes. This suggests that lakes, and especially artificial lakes, are not particularly good habitats for aquatic plants. It should be emphasized that the present study does not constitute a study of the aquatic plants of Oklahoma but only the plants of Oklahoma lakes. There is still a great need for a comprehensive survey of the higher aquatic plants of Oklahoma.

Only one past list of plants in any one Oklahoma lake is available for comparison with the present lists to determine what changes have occurred. Leake (1945) in a study of the algae of Crystal Lake, near Norman, Oklahoma, listed the hydrophytes in the lake. In her investigation the only hydrophytes listed were *Chara* spp., *Castalia tuberosa, Potamogeton amplifolius, P. foliosus macellus, Sagittaria latifolia, Typha latifolia, T. truxillensis,* and *Marsilea mucronata.* The hydrophytes in the present study (1945, 1950), however, included the following dominants from deep water shoreward: *Ceratophyllum demersum, Potamogeton nodosus, Eleocharis quadrangulata crassior, Polygonum coccineum pratincola, Scirpus validus creber, Eleocharis macrostachya, Lippia lanceolata recognita, Paspalum distichum, Juncus interior,* and *Juncus torreyi.* In Leake's investigation (1942, 1943) only *Potamogeton amplifolius* (probably what we have called *P. nodosus*) and *Eleocharis quadrangulata* are mentioned. In the present study, we did not encounter *Potamogeton foliosus, Sagittaria latifolia, Typha latifolia,* or *T. truxillensis* and observed very little *Chara.*

Certain of Leake's statements are worth quoting. She states that "the cattails, *Typha truxillensis* L. and *T. latifolia* L. flourish along the east margin except in seasons of extreme drought. At such times they are apt further to be injured by the practice of burning off the land." No cattails were observed during the period of our investigation. She points out that "at the east end of the lake, a patch of the white water lilly, *Castalia tuberosa* (Paine) Greene, occupies about three square yards of space. This plant

was probably placed here at some time in the past by the owner of the lake. At the present time the plot is about 30 feet in diameter. In her discussion of her collecting stations, she mentions *Chara* and *Potamogeton* several times but never acknowledges the presence of *Ceratophyllum*. By 1949, *Ceratophyllum* was so abundant as to constitute a considerable impediment to fishing. In view of the above statements and experience, it appears probable that many changes have occurred along the shoreline of the lake during the seven years between investigations.

The 420 species encountered in the survey were dispersed throughout 245 genera and 83 families. Families in groups, other than the angiosperms, included the Characeae (Thallophyta), Marsiliaceae and Salviniaceae (Pteridophyta), and Pinaceae (Gymnospermae). Of the 79 families in the Angiospermae, there were 12 monocotyledonous and 67 dicotyledonous families. The percentage of monocot families in the present survey (15) is about the same (17) as that in Gray's Manual (Fernald 1950).

The Cyperaceae, Gramineae, and Juncaceae were the monocotyledonous families with the greatest number of species per family. Many of the remaining monocotyledonous families (Alismataceae, Lemnaceae, Pontederiaceae, Typhaceae, and Zosteraceae) were composed predominantly of aquatic species. In order of decreasing number of species, the important dicotyledonous families were as follows: Compositae, Chenopodiaceae, Euphorbiaceae, Leguminosae, Onagraceae, Labiatae, and Scrophulariaceae. This list differs from the typical terrestrial list of plants in the relative importance of the Chenopodiaceae and Euphorbiaceae, and the relatively low position of the Leguminosae. All dicotyledonous families, except the Chenopodiaceae, include more terrestrial than wetland species, and very few of these families have any aquatic species.

There are some noteworthy variations in the east-west distribution of the species of given families. As might be expected, the species of families of woody plants were most numerous in the Eastern section and gradually decreased westward. The relative importance of the Cyperaceae and Juncaceae also decreased westward and no species of the Juncaceae were encountered in the Panhandle. On the other hand, the Gramineae, Chenopodiaceae, and Compositae were represented by an unusually large number of species in the Panhandle section.

## Wildlife Production

On the basis of utilization, water may be diverted from the lakes or remain therein. Diverted water is used for domestic, municipal, and industrial purposes such as manufacture, irrigation, and power. Stored water is typically utilized for flood control, recreation, and wildlife production. The production of wildlife in Oklahoma lakes, with relation to rooted aquatic plants will be discussed in the following order: fisheries, migratory waterfowl, and aquatic mammals.

The relation of higher aquatic plants to fishing is still uncertain. The practice of the Chinese, over 2,000 years ago, was to grow fish in a pond for about two years, then to empty the ponds and start over again with a basin devoid of plants. However, the practice in the early twentieth century (and still continuing to some extent) has been to recommend the planting of shallow ponds with such submerged aquatics as *Ceratophyllum*, *Myriophyllum*, and *Potamogeton*. Swingle and Smith (1932), however, suggested that aquatic plants be kept out of ponds since they decreased fishability and resulted in the production of small fish by providing them hiding places from larger, predaceous fishes.

The arguments for rooted macrophytic plants in fishing ponds and lakes include: increase in fertility, decrease in turbidity, increased oxygen supply (by submerged

plants), and an increased food supply. On the other hand, the higher aquatic plants protect young fish, which results in many small fish, decrease fishability, reduce oxygen tension (by floating plants), and decrease the length of life of the pond or lake. Although the value of rooted, macrophytic plants is not yet established with certainty, it is the feeling of the writer that macrophytic aquatic plants do more harm than good in a pond or lake designed primarily for fisheries production.

A concerted effort is being made in Oklahoma to increase the hunting of ducks and geese. Mahaffey (1949), in discussing the Tishomingo National Wildlife Refuge, states that plantings of millet, smartweed, sedge, and a tremendous amount of submerged aquatics have been made "to lure the wild ducks in." One of the difficulties encountered at the Tishomingo Refuge is the variable level of Lake Texoma which, in one year's time, "has fluctuated as much as eighteen feet" (Mahaffey 1949). In 1943, Mitchel conducted a survey related to existing vegetation types and made planting recommendations for 197 creeks, coves, and miscellaneous areas of Grand Lake. Regarding these plantings the Oklahoma Game and Fish Department (1950) reported that "In isolated instances the seeding was partially successful; but, in general, it was not considered worthwhile. The fluctuating water level and the presence of so much barren shoreline prevent the establishment of stabilized aquatic and semi-aquatic plant growth on a large scale." Martin and Uhler (1939) concluded that "no single factor is more potent in preventing the development of waterfowl feeding grounds than extreme or irregular fluctuations in water level." After having reviewed the results of seeding and transplanting hydrophytic waterfowl food plants in Louisiana, in the Tennessee Valley, and in Oklahoma, it is believed that such plantings will never be successful in lakes with wide amplitude of water levels (Altus, Canton, Fort Supply, Grand, Salt Plains, Texoma, and Wister Reservoirs).

Little is known about the plantings of hydrophytic waterfowl food plants in constant level lakes in Oklahoma, but such plantings should be relatively successful when compared to those attempted in fluctuating lakes. The admonition of Addy and MacNamara (1948) should be followed, *viz.:* that, since "Plants growing is a mature habitat are generally the ones best suited to compete and survive in that particular place under existing conditions" plantings in long-established ponds usually "should be restricted to new or altered places."

"The fur trade has never figured among the important industries of the state" (Duck and Fletcher 1943). Of the annual total value of pelts, the aquatic mammals furnish a relatively small percentage, the important ones being as follows: mink, 9.75; muskrat, 4.39; and raccoon, 3.72. Mink is found associated with all major water systems of the state, and is "known to react favorably to various watershed improvements such as pond building and lake construction" (Duck and Fletcher 1943). Raccoon populations have been increased considerably through such management practices as protection of woodland from grazing and burning, construction of small dams on creeks to increase food supply, protection of natural den trees and construction of artificial dens. Most of the muskrat pelts come from the northern two-thirds of the state. The most unfavorable factor is the unstable water level of most of otherwise suitable muskrat habitats. This variable water level prevents the ecesis of muskrat food plants, such as species of *Scirpus* and *Typha,* and interferes with the home activities of the muskrat. With the greatly increased water surface in the state, there is no doubt that a tremendous increase in aquatic mammal population could be ef-

fected if reasonable management practices could be instituted.

### Plant Control

As is well known by this time to the reader, constant level pools are distinguished by excellent zonation and an abundance of plants whereas fluctuating lakes are characterized by poor zonation and a paucity of all except terrestrial plants. This suggests that water may be utilized as an effective agency in the control of plants. Hinman and Hess (1949) reported that "it has been possible through improved water level management schedules to reduce the extent of invasion in the main Tennessee river reservoirs from about five feet to slightly over a foot." As a matter of fact, water-level manipulation has been utilized regularly since 1942 for the control of plants in the reservoirs of the Tennessee Valley Authority. Since most of the water bodies in Oklahoma are subject to water level manipulation, it is obvious that the control of terrestrial, wetland, and aquatic plants by the management of water levels should be a simple procedure. In natural lakes and in artificial lakes where a constant pool level is desired other physical methods or chemical and biotic means of control must be employed. Of the physical methods, increased turbidity by the use of aniline dyes has been employed (Eicher 1947). Other means include direct attack on the plants such as removal, underwater cutting, mowing, and crushing. At Reelfoot Lake, Tennessee, *Zizaniopsis miliacea* was reduced by lowering the water in the winter-time and "burning grass remains so as to expose rootstocks to freezing" (Steenis 1950). *Ceratophyllum demersum* was controlled by holding the water levels high and allowing wind and wave action to clear open areas of this unanchored plant.

Chemicals used in plant control include ammonium sulfamate, sodium arsenite, sodium chlorate, and 2, 4-dichlorophenoxyacetic acid (and related chemicals). To date 2, 4-D has proven to be the chemical of choice in the control of terrestrial wetland, emergent and floating leaf plants. "Most species studied were found to be most susceptible to 2, 4-D formulations after full summer foliage was reached until fall" (Hall and Hess 1950). 2, 4-D was found to be effective for the following species, all of which are common in Oklahoma lakes: *Ambrosia trifida texana, Campsis radicans, Justicia americana, Juncus effusus solutus, Jussiaea repens glabrescens, Nelumbo lutea, Salix nigra,* and *Xanthium italicum.* Up to the present time, no chemicals have proven practical in the control of submerged plants.

Of the biotic factors, grazing is moderately effective in controlling wetland and emergent aquatic plants, but only when the grazing pressure is sufficient to produce overgrazing in the main body of the pasture. Fire has been utilized for wetland and emergent aquatic plants at times of considerable recession. It has been fairly effective for woody plants but rarely destroys the underground parts of herbaceous, perennial plants. An interesting development in recent years is the control of floating leaf and submerged plants by fertilization. This increases the phytoplankton, zooplankton, and filamentous algae to such an extent that the macrophytic plants are shaded out. "Normal fertilization after the emergent plants are destroyed will prevent the growth of submerged weeds in all except the shallowest water" (Swingle and Smith 1942).

### Summary

1. The plant populations of thirty-two lakes in Oklahoma were investigated during the summers of 1948, 1949, and 1950.

2. The lakes are distributed throughout Oklahoma as follows:

a. Eastern section (94° 30′ W-96° W)—Six reservoirs and four oxbows.

b. Central section (96°-98° W)—Eight reservoirs.

c. Western section (98°-100° W)—Ten reservoirs.

d. Panhandle (100° W-103° W)—Four playas.

3. The most important climatic factors in determining the distribution of lake plants appear to be precipitation and evaporation.

4. Of the lake basin factors, amplitude of water levels and turbidity are paramount. These factors are, in turn, largely controlled by man's agricultural activities and the procedures he utilizes in reservoir maintenance.

5. The parts of the lake basins investigated were: a. drift lines, b. flood surcharge zone, c. summer pool level, d. recession zone, and e. continuous water area.

*Communities*

6. A total of 48 plant communities was observed, distributed according to habitat as follows: terrestrial, 13; wetland, 15; and aquatic, 20.

7. Of the six woody communities encountered, three occurred in the flood zone and three at the summer pool level. None was present in the Panhandle section. The *Salix-Tamarix* associes occurred in more lakes (22) than any other woody or herbaceous aggregation.

8. On drift lines only herbaceous terrestrial communities were encountered, those studied being in the Panhandle section.

9. Of the herbaceous communities in the flood surcharge zone, terrestrial aggregations were the most numerous, but wetland and even aquatic aggregations may be present when water remains in the flood zone for a sufficient period during the growing season.

10. Communities at the summer pool level included three herbaceous wetland and one aquatic aggregations.

11. In the recession zone, following a prolonged drop in water level, a number of terrestrial and wetland communities become established below the wetland fringe and even below the emergent aquatics. Six other communities, typical of other zones, also occur here under these conditions.

12. In the recession zone, with little or no drop in water level, eight emergent aquatic communities become established, the most numerous being the *Justicia americana* and *Typha domingensis* consocies (10 lakes each).

13. Communities of continuous water area comprised pleustonic, floating leaf, floating mat, and submerged aggregations. Such communities are rare or absent in reservoirs designed for flood control, and in the playas of the Panhandle.

14. Salt water communities were encountered only in the Salt Plains Reservoir of the Western section.

*Species*

15. The total list of species observed was 420, of which 182 each were terrestrial and wetland plants and only 56 were aquatic species. These facts suggest that artificial lakes are not particularly good habitats for aquatic plants.

16. The number of species was about equal in the Eastern, Central, and Western sections, but was relatively low (one-third as many) in the Panhandle. Of 210 species in the Eastern section, only 12 were encountered in the Panhandle.

17. In comparing the plant lists of Crystal Lake for 1942 and 1943 with those of 1949 and 1950, it was observed that many changes had occurred, including the disappearance of *Typha,* the virtual disappearance of *Chara* and a tremendous invasion of *Ceratophyllum.*

18. The 420 species sampled were dispersed throughout 245 genera and 83 (12 monocot, 67 dicot, 4 other) families. Monocot families included more wetland and aquatic species whereas dicot families comprised relatively more terrestrial plants.

*Wildlife production*

19. It is suggested that macrophytic plants are unnecessary, and in most cases are undesirable, in ponds or lakes designed primarily for fisheries production.

20. It appears probable that the planting of waterfowl food plants is relatively successful in constant-level lakes but should not be attempted in lakes with wide amplitude of water levels such as flood control reservoirs.

21. Plant control procedures are necessary only in constant-level pools. 2, 4-D herbicides apparently provide the best hope for the control of lake plants except for submerged species.

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# STUDIES ON THE HELMINTH FAUNA OF ALASKA. XIII. DISEASE IN THE SEA OTTER, WITH SPECIAL REFERENCE TO HELMINTH PARASITES

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## INTRODUCTION

During the spring of 1951, the U. S. Fish and Wildlife Service undertook the removal of sea otter, *Enhydra lutris* (L)., from the Aleutian Island of Amchitka, for the purpose of restocking range from which the animals have long been exterminated. The decision to undertake this activity was influenced by the nature of military operations planned for the island later the same year. The capture and removal of the otter were under the supervision of Mr. Robert D. Jones, Biologist, U. S. Fish and Wildlife Service. Heavy losses among the animals shortly after capture made the venture unsuccessful. Many deaths were concurrent among animals in the wild state. The writer was asked to investigate the causes of disease in the sea otter, and it is the purpose of this paper to report the results of these investigations.

### *Status of the Sea Otter*

The numerical recovery of the Aleutian sea otter populations has been very good in recent years, and some thousands of animals now occur in Alaskan waters. Their distribution, however, is discontinuous and much of their former range is unoccupied. This fact implies a slow rate of redistribution from the existing population centers. Sea otter are numerous around the islands comprising the Rat and Andreanof groups. The greatest known concentration is around the island of Amchitka, one of the Rat Islands.

Sea otter are likewise reduced in range and numbers in Asiatic waters. According to Bobrinskii *et al.* (1944 p. 134), they are still numerous around the Komandorskii Islands and Kamchatka (Cape Lopatka). On Mednii Island, in the Komandorskii group, otter are numerous, and here a comprehensive study of sea otter bionomics was made by Barabash-Nikiforov (1935). The report of Steller (1749) contains much important information on the biology and habits of the sea otter. His observations were made mainly on Bering Island. Sea otter reportedly still exist in the Kurile Islands, but the writer has no recent information regarding their status.

The characteristics of population behavior of the sea otter are little understood. Such knowledge would seem to permit some evaluation of the relationships of population density to morbidity, since it is evident that some of the disease conditions reported herein are directly related to utilization of invertebrate animals for food. Progress in this connection will be dependent upon carefully-planned, long term investigations which utilize the best of modern techniques and trained personnel.

### *Amchitka—Characteristics of the Habitat*

This work is concerned exclusively with sea otter disease on the island of Amchitka. Situated well toward the western end of the Aleutian Island chain, Amchitka is unique in being low and relatively flat. The maximum elevation, about 1300 feet, is attained in hills at the west end of the island. Boulder-strewn beaches, often bordered landward by steep or cliff-like banks, surround the island for the greater part. Sandy beaches are few. Rock outcroppings jut into the sea and form precipitous cliffs.

The shore is broken by fjord-like clefts. Rocky flats are exposed at low tide, and these serve as the feeding and resting places of great numbers of waterfowl.

Numerous invertebrate animals occur in the tide pools and just outside the tidal zone. Conspicuous forms are *Mytilus edulis* L., *Littorina atkana* Dall, *Acmaea digitalis* Eschscholtz, *Katherina tunicata* Wood, and *Strongylocentrotus dröbachiensis* (Müller). Marine algae grow luxuriantly around the island, with *Alaria, Nereocystis,* and *Fucus* most plentiful. Fishes are abundant, and one of the most common forms, according to collecting results, is a greenling, *Lebius superciliosus* (Pallas). Various species of sculpins (Cottidae) are also numerous.

Great quantities of algae and animal remains are deposited by the sea in windrows well up on the shores. Such debris may extend into the zone grown to rye grass, *Elymus arenarius mollis* (Trin.) Hult., which usually covers the banks and certain other areas, such as sites of old Aleut habitations. Rats, *Rattus norvegicus* Berkenhout, and arctic foxes, *Alopex lagopus* L., both introduced by man, forage among this debris. The banks are much tunneled by the rats, and the description by Schiller (1952) of conditions existing on Adak Island applies well here. Hundreds of sea birds, particularly alcids, nest on offshore rocks. Landnesting birds, formerly abundant, have been much reduced, apparently through the depredations of rats and foxes—another example of the results of introducing exotics without thought of the consequences. Pinnipeds are numerous. The harbor seal, *Phoca vitulina* L., is the most abundant, and Steller's sea lion, *Eumatopias jubata* (Schreber), is locally common. These animals are found in the same localities as the sea otter and in some places use the same hauling-grounds.

An estimate of three to four thousand sea otter on Amchitka may not be unreasonable, although the actual number is not known. Otter appear to be distributed around the entire island, but not uniformly so. Some aggregations of otter are relatively large, and it appears that, for much of the year, these retain their identity. Thus, a group of about 130 otter was regularly observed a few miles west of Kirilof Bay in the spring of both 1951 and 1952. Observations made both earlier and later by other workers indicated no change in this behavior. Little is known, however, of summer and fall activity. Besides such obvious concentrations of animals, smaller groups and single individuals may be seen at any time along the shores of Amchitka.

The feeding habits of sea otter have been the subject of considerable study. The report of O. J. Murie (1940) includes information on diet composition and other phases of the bionomics of this animal. Jones (1951) has presented general information on the Amchitka sea otter. Details on the diet need not be discussed in this paper, except where pertinent to the following consideration of parasite life cycles.

## Acknowledgments

The writer wishes to express appreciation of aid rendered in connection with this work by the following: Messrs. Robert D. Jones, Paul Adams, Russell R. Hoffman, W. K. Clark, and David Hooper, biologists with the U. S. Fish and Wildlife Service, assisted in various ways with the field work on Amchitka; Mr. E. L. Schiller, of this laboratory, studied the nematode material collected; Miss Reggie V. Sacressen, of this laboratory, prepared the histological sections and drawings of *M. pirum.* Thanks are also expressed to Dr. Rue Jensen, Colorado A. and M. College, for reviewing certain slides, and to Miss Thirza Donnegan, Alaska Department of Health, for the evaluation of hematological material.

The U. S. Fish and Wildlife Service supported the cost of the field work on

Amchitka. Without this cooperation, the work would not have been possible.

## Materials and Methods

Three animals were examined by the writer in 1949. Losses were relatively light this year, and the animals, having been found dead on the beach, were not in suitable condition for study. In 1949 no particular significance was attached to the few deaths known to have occurred on Amchitka.

No losses were reported in 1950. Heavy losses, however, occurred in February, 1951, and continued through this month and early March. The writer arrived on Amchitka March 19, 1951. Dead otter were still numerous, but by this time numerous deaths were no longer occurring. On March 19, the writer observed 14 dead otter along a two-mile stretch of beach. These animals were in such condition as to be of little value for detailed examination. Many dead animals were examined, but only 19 were obtained in acceptable condition.

During March, 1952, the writer spent ten days on Amchitka. Fish and Wildlife Service personnel had been there some weeks prior to this time, and it was agreed that only light losses had occurred during late winter, 1952. Eight animals in suitable condition for study were obtained. Mr. David Hooper, U. S. Fish and Wildlife Service, examined a few more after the writer's departure. Mr. E. L. Schiller, of this laboratory, continued observations in May and June, 1952, but noted only a few remnants of sea otter carcasses, believed to be animals which had died during the previous winter or early spring.

Most of the data included herewith were obtained by the writer through the *post mortem* examination of sea otter in the field, together with later laboratory study of materials collected. As is noted, it was not possible to obtain an adequate number of otter in condition suitable for study. Because of the strict regulations governing the slaughter of the animals, normal otter could not be utilized in connection with this investigation.

Morbid animals were occasionally found on the beaches, where they could be readily captured. Other animals, considered normal when captured, became morbid in captivity. In either case, death of the animal was the final outcome. It is not possible at this time to evaluate the effect handling, artificial food, and confinement might have on the captive otter. There is some indication that captivity has an adverse effect, but further investigation is required.

All captured otter were confined in wire enclosures around fresh-water tundra ponds, or in cages. Captive animals were observed closely in order to record clinical symptoms of diseases affecting them. Because of the diversity of conditions present, such observations had little value.

Almost all of the sea otter obtained during the course of this work were subadults. Twenty-eight ranged in weight from 3.7 to 73 lbs. The average weight was 34 lbs. Four animals were considered normal; these were a cub (3.7 lbs.), a large male (73 lbs.), and two females (51 and 33 lbs.). Besides these, only two more females were obtained. The heaviest mortality occurred, on the basis of this, in subadult males. An abnormal sex ratio was evident.

Animals dying in captivity were autopsied as soon as possible after death. Several otter found dying upon the beaches, as well as captive animals in the terminal stages of disease, were killed to obtain material more suitable for study. Detailed examination of such animals was made in the field, and appropriate tissue specimens were collected for later histopathological study. Inoculations of bacteriological media were made from various organs at the time of autopsy. Preliminary incubation of this material was carried out on Amchitka, but all further work was completed in the laboratory at

Anchorage. Blood smears were made routinely from the living animals, and blood serum was collected whenever possible.

Tissues for histopathological study, after fixation in either formalin-acetic acid-alcohol or ten per cent formalin, were embedded by the paraffin method. Sections were stained routinely with hematoxylin-eosin and Mallory's aniline blue stain. Heidenhain's azan stain, Turnbull's blue method for hemosiderin, Lee-Brown's modification of Mallory's aniline blue stain, Unna's differential stain for mast and plasma cells, and Mallory's fuchsin stain for hemofuscin, were applied in special cases. Trematodes were stained in Ehrlich's acid hematoxylin or Semichon's acetic carmine stains. The nematodes were cleared for study in liquefied phenol.

## Results

The present investigation has revealed that the sea otter is subject to infection by a variety of helminth parasites. These affect the host to varying degrees—most appear to have little significance, but at least two are highly pathogenic. *Ante mortem* diagnosis of disease in sea otter will have to depend on the results of further, more intensive study. All parasites recorded from sea otter during this investigation are considered separately in some detail. In connection with certain of these parasites, appropriate remarks on taxonomy and morphology have been included. Details on helminth species occurence have been summarized for 31 animals. Other pertinent data are included.

### I. *Pyramicocephalus phocarum* (Fabricius, 1780)

Found but once in a 73 lb. adult otter, *P. phocarum* appears to be of rare occurrence in this host species. The specimen collected was only 58 mm. long, and sexually immature. Nothing could be observed regarding localization of this cestode in the host, since circumstances delayed for some time after death the examination of this animal. Upon autopsy it was found that all parasites present had relinquished any attachment to the host tissue. No gastric or intestinal lesion characteristic of the attachment of *P. phocarum* in other hosts was observed.

The writer had collected this species of cestode rather frequently from the bearded seal, *Erignathus barbatus* (Erxleben), along the Arctic Coast of Alaska. In the bearded seal, *P. phocarum* attaches itself to the muscosa of the pyloric region of the stomach. The highly specialized scolex is always deeply embedded in the tissue of the host, so that the cestode is pulled away only with difficulty. A crater-like lesion about 5 mm. in diameter is characteristically seen at the place of attachment. A mild tissue reaction occurs.

Barabash-Nikiforov (1935) recorded an unidentified cestode from Bering Island sea otter. Afanas'ev (1941) reported no cestodes from animals examined by him.

### II. *Orthosplanchnus fraterculus* Odhner, 1905

The most common parasite collected, *O. fraterculus* occurred in 28 of 31 otter examined. Nothing is known of the life cycle of this trematode, but it was concluded that otter regularly become infected during their first year of life.

The writer has observed *O. fraterculus* in both the gall bladder and pancreatic ducts of the bearded seal, but in the sea otter it appears to be limited in locus to the gall bladder. The sea otter gall bladder is somewhat specialized, and a few appropriate remarks regarding its structure are included herewith:

In the adult male otter, the gall bladder attains a maximum length of about 150 mm. It is elongate, with gradual enlargement toward the distal end; the maximum diameter is about 20 mm. Observations indicate that the sea otter gall

bladder is not capable of much contraction or expansion. The walls of the organ are relatively very thick. The muscular layer with the perimusclar connective tissue has a thickness of at least 4 mm. in the adult animals. This thickness is about equaled by that of the combined mucosa and lamina propria. The mucosa has many gland-like openings throughout, but the epithelium lining the majority of these is not glandular. According to staining results, it is possible that a few glands do occur in the mucosa of the body of the organ, but this needs further study. The relatively small quantity of bile observed in all animals examined by the writer has been somewhat viscous, with a slightly greyish or greenish tinge. The usually dark green color characteristic of bile has not been observed.

*Gross pathological changes.* Incision of the gall bladder disclosed the organ in most cases to be filled almost completely by hundreds of trematodes. These attach themselves firmly to the mucosa, with the posterior end projecting into the lumen. Fibrotic nodules of various sizes up to about 2 mm. were noted. Chronic infections, in old animals, resulted in extensive fibrosis. Fibrocytic proliferation may bring about occlusion of the gall bladder lumen. This would seem to be further evidence that the organ changes its state of contraction very little.

*Histopathological observation.* Transverse sections of the gall bladder showed that the trematodes attach themselves by taking into the oral and ventral suckers a considerable quantity of host tissue. *O. fraterculus* has an integument armed with sharp spines about 16 μ long. These spines cause chronic irritation of the mucosa, with the resulting above mentioned fibrosis (Fig 1.). Mucosa hypertrophy may also be characteristic of *O. fraterculus* infections. Adequate material from non-infected otter for comparison was not available to permit a decision on this point. Trematode eggs were often seen entrapped by the host tissue reaction (Fig. 2). Mononuclear cells infiltrated immediate areas surrounding the trematodes, and also the eroded superficial layers of mucosa. Hyperemia was never marked.

*Pathogenicity.* While *O. fraterculus* is mildly pathogenic, there is no evidence suggesting an important effect on the host. The occlusion of the lumen of the gall bladder does not appear to bring about serious changes. Accumulation of bile distal to the occluded portion was not observed. No tendency toward occlusion of the cystic duct was noted.

### III. *Phocitrema fusiforme* Goto and Ozaki, 1930

As a parasite of the sea otter, *P. fusiforme* seems to have no importance. The writer has collected it but once from otter, but it occurs frequently in Aleutian Island foxes. A second record of this trematode from the sea otter was obtained by Mr. David Hooper, U. S. Fish and Wildlife Service, during late March, 1952. The animal examined by him was very young, weighing only 12 lbs., and was still in company of an adult female. In addition to Amchitka foxes, two foxes from the island of Kiska were found to harbor *P. fusiforme*. Afanas'ev (1941) recorded this trematode from the fur seal, *Callorhinus ursinus* L., in the Komandorskii Islands.

### IV. *Pricetrema zalophi* (Price, 1932)

Of rare occurrence in the sea otter, *P. zalophi* has no apparent effect upon the host. This minute trematode was recorded but once by the writer from Amchitka sea otter, and it was not collected from any other host species. The life cycle of *P. zalophi* is unknown.

### V. *Microphallus pirum* (Afanas'ev, 1941)

(Syn. *Paraheterophyes pirum* Afanas'ev, 1941; *Microphallus enhydrae* Rausch and Locker, 1951.)

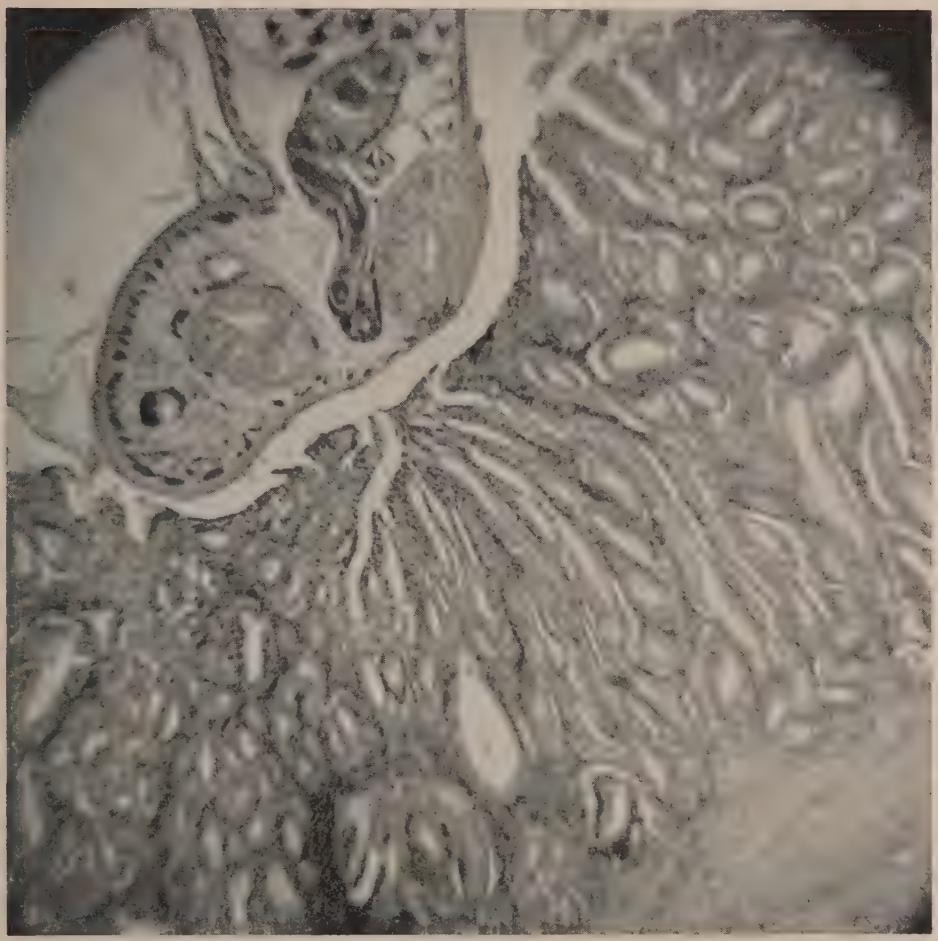

FIG. 1. Transverse section of sea otter gall bladder with specimen of *Orthosplanchnus fraterculus in situ.* Low power.

First recorded from the intestine of sea otter and arctic foxes on Bering and Mednii Islands (Afanas'ev 1941), *M. pirum* is a common and important parasite of sea otter on Amchitka. It was collected from 21 of 31 animals studied in detail.

Without knowledge of Afanas'ev's paper, this trematode was described by Rausch and Locker (1951) as *Microphallus enhydrae.* Dr. James E. Lynch, School of Fisheries, University of Washington, called to the writer's attention the report of Afanas'ev. Some discussion of the taxonomic status of the trematode is pertinent here.

A new genus, *Paraheterophyes,* was erected by Afanas'ev (1941) for the single species, *P. pirum.* Among related genera *Paraheterophyes* was differentiated only from *Heterophyes* Cobbold, 1866. Afanas'ev stated (p. 97) that " . . . it differs from this genus in having a different arrangement of the uterus, of the testes, vesicula seminalis, and in several other characters." The genus *Microphallus* Ward, 1901, was not considered, al-

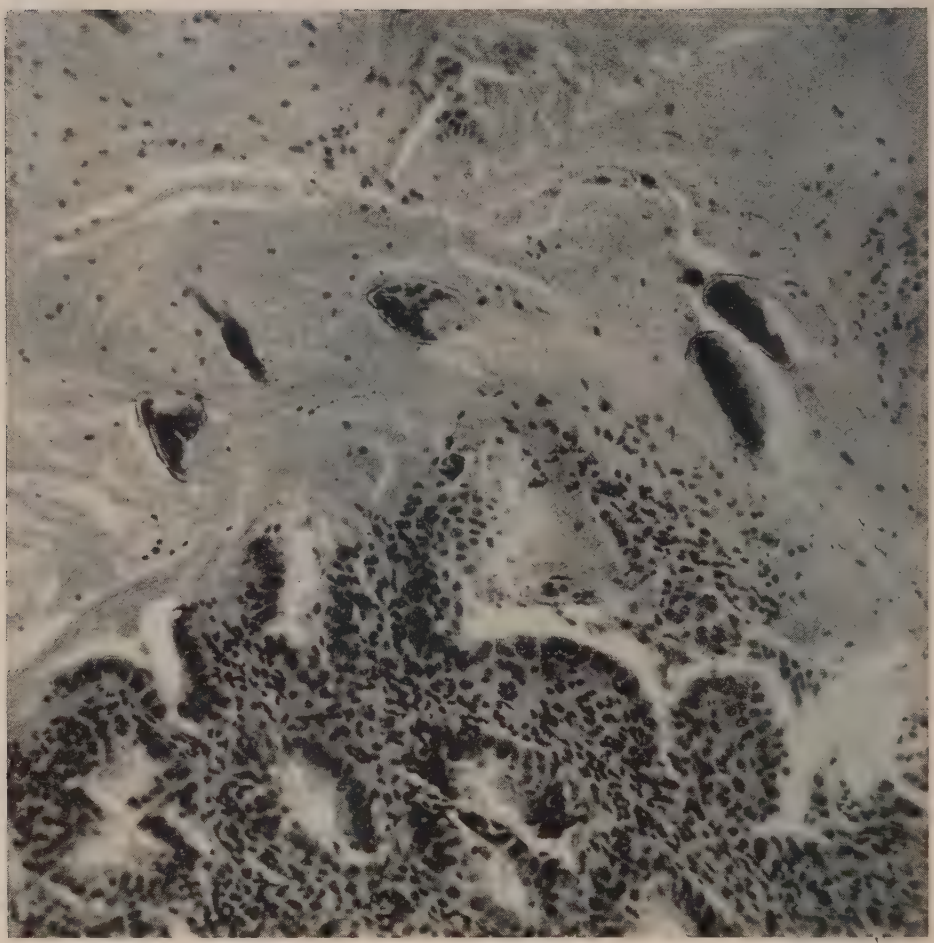

FIG. 2. Sea otter gall bladder showing fibrosis and entrapped eggs of *Orthosplanchnus fraterculus*. High power.

though, in the writer's opinion, Afanas'ev's species clearly belongs here.

The original Aleutian material was obtained by the writer from otter found dead upon the Amchitka beaches and subsequently stored for some weeks in a frozen state. The trematodes had degenerated, and this gave rise to certain inaccurate interpretations of morphological details. The later opportunity for the collection of living worms provided an abundance of material in condition for study. Serial sections of the trematodes *in situ* were also prepared. A drawing of an entire specimen of *M. pirum*, and details of the genital ducts, are included (Figs. 3-5).

The study of this additional material has disclosed nothing which would invalidate its assignment to *Microphallus*. It should be pointed out that the cuticle of *M. pirum* is, as described by Afanas'ev, thickly beset with spines. The Komandorskii Island specimens averaged somewhat larger than those from Amchitka, but rather remarkable size variation in the species of *Microphallus* appears to be the rule (Rausch 1947).

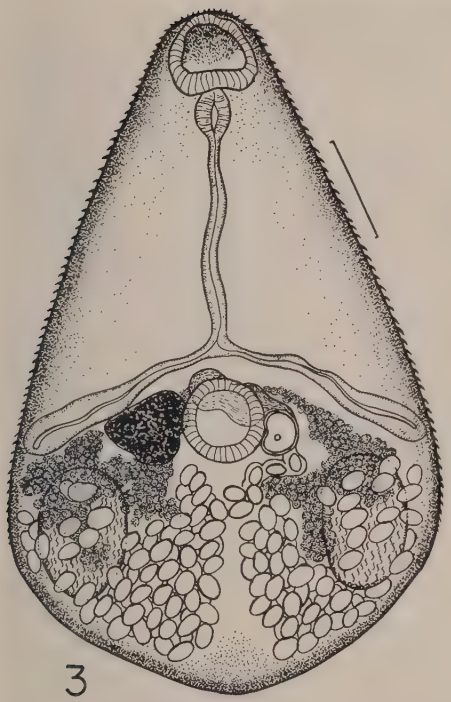


FIG. 3. *Microphallus pirum,* entire specimen, ventral view; from sea otter intestine. Scale has a value of 60 μ.

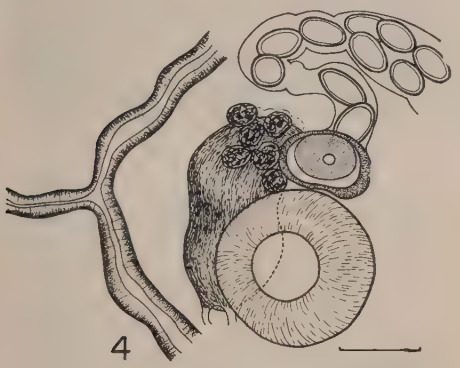


FIG. 4. Enlargement of terminal portions of genital ducts of *Microphallus pirum.* Scale has value of 30 μ.

The recent papers by Cable and Kuns (1951) and by Stunkard (1951) did not consider *M. pirum* in any detail; these workers also were apparently unaware of Afanas'ev's publication.

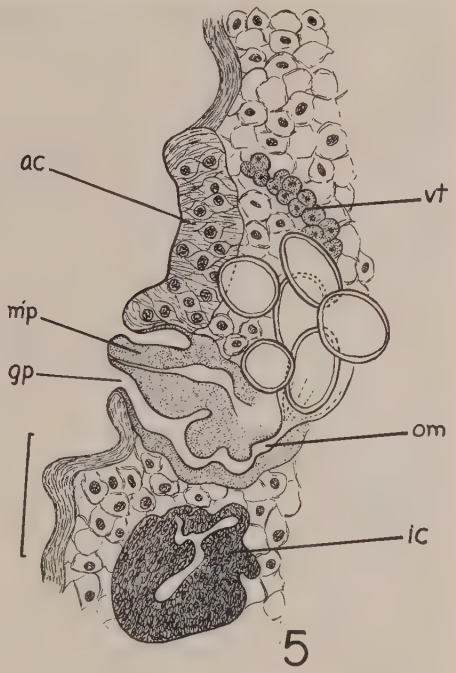


FIG. 5. Oblique section through acetabulum and genital pore of *Microphallus pirum.* AC—acetabulum; MP—copulatory papilla; GP—genital pore; VT—vitelline gland; OM—end of metraterm; IC—intestinal cecum. Scale has value of 30 μ.

The entire life cycle of *M. pirum* is unknown. Afanas'ev assumed some species of fish to be the second intermediate host, but the writer thought it to be a crab. The writer was unsuccessful in the collection of crabs on Amchitka; however, Mr. E. L. Schiller, of this laboratory, during May and June, 1952, collected a series of hermit crabs from tide pools. These he found to be infected by the metacercarial stage of *M. pirum.* Schiller (1953) has reported his work separately.

*M. pirum* is no doubt pathogenic, but its true effect on the sea otter host may have been in part obscured by the presence of another pathogen. Consequently, the following descriptions are written with the realization that some of the pathological changes observed may not be attributable to *M. pirum* alone.

*Gross pathological changes.* An enteritis of varying degrees of severity was observed in every case with the presence of moderate to great numbers of trematodes. Semi-fluid excreta containing a large proportion of blood were characteristic. *Post mortem* examination of such animals disclosed marked hyperemia of the villi, and the dark brown to blackish color of the intestinal content indicated much extravasation of blood. Gastritis, relatively mild, was noted in the majority of cases. In particularly severe cases of enteritis, exudate containing much fibrin was closely adherent to the mucosal surface. The trematodes, occurring only in the small intestine of the host, were distributed through the layer of exudate which adhered to the mucosal surface. They occurred also in the exudate in the lumen, but were relatively fewer here. The trematodes appeared as minute, dark bodies on the mucosal surface; the dark-colored eggs in the voluminous uterus of *M. pirum* alone being visible, since the remainder of the worm's body is transparent. (The trematode body averages less than 500 μ in length.) A maximum number of 30 trematodes per square mm. of mucosal surface was counted (in a cleared gross-section of intestine).

*Histopathological observations.* Severe mucosal hyperemia was characteristic, as was extensive desquamation of mucosal epithelium. Trematodes occurred at all levels in the intestinal wall (Fig. 6). The greatest numbers occurred in the mucosa, but some had penetrated the muscularis externa. Complete intestinal perforation was observed, with trematodes localized on the serosal surface. In such cases a slight inflammatory reaction had been evoked, with fibrocytic proliferation and invasion by mononuclear leukocytes. Polymorphonuclear neutrophils were absent. Within the intestinal wall, fibrosis around the trematodes was not noted. There was also little or no leukocytic infiltration, indicating that the trematodes were actively migrating through the tissue. This impression was further supported by evidence of mechanical damage to the mucosa. Trematodes were fewer, and were more superficially localized, in the lower part of the small intestine. Bacteria were not much in evidence anywhere, and were not seen invading the living tissue along with the trematodes. Trematode eggs were not observed in the intestinal tissue. No lesions in other organs were noted which could be attributed to *M. pirum* infection.

*Pathogenicity.* On the basis of mechanical damage alone, brought about by the movements of the trematodes, it would appear that *M. pirum* has an important pathogenic action. The cuticle of *M. pirum* is beset with great numbers of recurved spines which must contribute much to the irritation of the host tissue. If the observations have been correctly interpreted, it would seem that the degree of pathogenicity is directly proportional to the number of trematodes present. Trematodes of all ages, including newly ingested, but excysted, metacercariae, were regularly seen in a single animal, indication that there may be a constant increase in number.

*M. pirum* appears to behave much as various species of heterophyid trematodes in that extensive mucosal invasion takes place before maturity, but the parasites return after maturing to the intestinal lumen. This concept is supported by the lack of eggs in the host tissue. In cases where trematodes are localized permanently deep within the host tissue, free eggs entrapped by the tissue reaction of the host are usually observed. Willey and Stunkard (1942) reviewed the tissue-invasion behavior of various heterophyid species in the definitive host, and also investigated fully the life cycle and pathogenicity of a heterophyid trematode, *Cryptocotyle lingua* (Creplin 1825). They reported heavy losses caused by *C. lingua* among young foxes. These workers

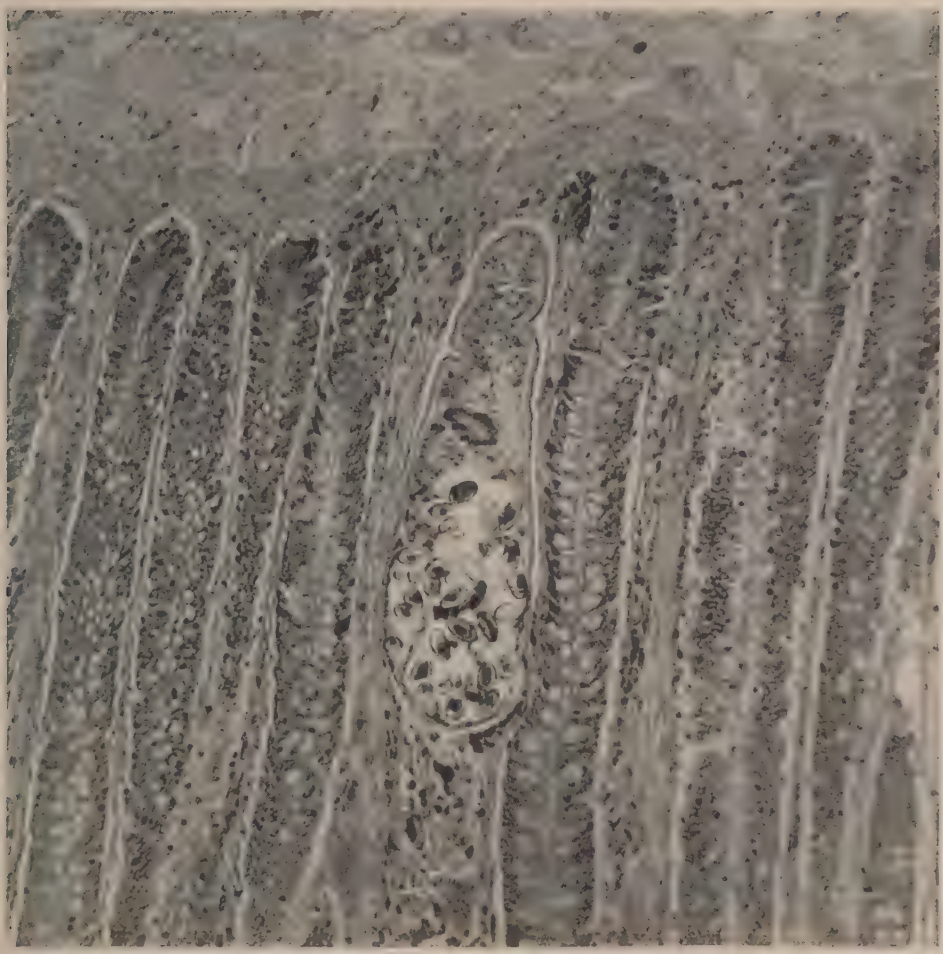

FIG. 6. Specimen of *Microphallus pirum* in mucosa of sea otter intestine. Low power.

were able to produce fatal experimental infections of large adults dogs by feeding fishes harboring the metacercarial stage of *C. lingua.* They summarized the effect of the parasites on the dog intestine as follows: "They denude the epithelium, produce a copious exudation of mucus, cause pressure atrophy, necrosis, sloughing of tissue, hyperemia, infiltration of eosinophils and plasma cells, and hyperplasia of the fixed tissue elements. The damage is largely mechanical and limited to the surface of the villi and the region between them." If anything, the effect of *M. pirum* on the sea otter is more severe, since the degree of tissue invasion is much greater.

The writer has no evidence that the eggs of *M. pirum* are ever distributed by the bloodstream of the host, with resulting serious effect, as was described by Africa *et al.* (1935), for certain heterophyid trematodes (*Monorchotrema taichui* Nishigori, 1924; *M. taihokui* Nishigori, 1924; *Diorchotrema pseudocirrata* Witenberg, 1929; *Heterophyes breviceca* Africa and Garcia, 1925). These trematodes invade the intestinal mucosa of man or other mammals.

Cordy and Gorham (1950) studied the

effect of *Troglotrema salmincola* (Chapin, 1926) on the host intestine. The pathological changes brought about by the trematodes *per se* resembled in general those observed in *M. pirum* infections, although not so severe.

Afanas'ev (1941) recorded also *Nanophyetus* sp. (= *Troglotrema* sp.) from Komandorskii sea otter. This species was not recorded from Aleutian animals.

### VI. *Porrocaecum decipiens* (Krabbe, 1878)

During the present investigation but one species of nematode, *Porrocaecum decipiens,* was recorded from Aleutian Island sea otter. It has been reported from the same host by Barabash-Nikiforov (1935) and Afanas'ev (1941), in the Komandorskii Islands. A larval specimen of *Porrocaecum* sp. was collected by O. J. Murie (Murie *et al.*; ms.) from an otter taken on Ogliuga Island.

The name *Porrocaecum decipiens* is applied here, although its validity is somewhat controversial. A discussion of the nomenclatorial status of this nematode has been presented by Johnston and Mawson (1945, pp. 110-116). A detailed description of *Ascaris decipiens* (=*P. decipiens*) was published by Stiles and Hassall (1899, pp. 109-120). These workers also summarized from the literature a list of mammals from which *P. decipiens* has been recorded.

The life cycle of *P. decipiens* has been investigated by several workers. Various species of fish serve as the intermediate host. Around Amchitka, according to the observations of E. L. Schiller, a greenling, *Lebius supercilosus* (Pallas), often harbors the larvae of *P. decipiens.* Other species are no doubt also infected here. The writer has observed sea otter at the surface with still-living greenlings, upon which they were feeding, and others also have made observations which imply that the sea otter capture fishes rather readily. Fish remains appear frequently in sea otter excreta.

Important losses in sea otter no doubt occur as the result of nematode infection. *P. decipiens* is sometimes highly pathogenic in the larval stages, although the adult worms seem to have no deleterious effect upon the host. According to present knowledge, the nematodes may be divided into three groups, according to degree of pathogenicity:

1. The earliest stage found in sea otter (*i.e.,* worms having a cephalic spike) appears to be the most pathogenic. This larval stage was always associated with intestinal perforation and seemed directly responsible for all sea otter deaths known to have resulted from nematode infection (Fig. 7).
2. Later larval stages, possessing fully developed lips, but still sexually immature, were usually found attached in closely associated aggregations in the sea otter stomach. These are considered only mildly pathogenic (Fig. 8).
3. Adult worms, not commonly found, appeared to be nonpathogenic. Nematodes in the adult stage were not observed attached to the mucosa of the stomach nor associated in any way with intestinal perforation.

*Symptomatology.* It was not possible to define clearly the symptoms associated with nematode infection in sea otter. Lack of diarrhea served to differentiate such animals from those suffering from the other two enteric conditions observed. Otter captured in the terminal stages of nematode infection showed depression and weakness. They often fed readily up to a few hours preceding death. Old adult otter as well as young animals were affected by *Porrocaecum* infections.

Since most of the life of the sea otter is spent in a marine habitat, the animals are not well adapted for extra-aquatic activities. Their abdominal muscles are relatively flaccid, and the visceral organs are not firmly supported. As a result, it would seem that the rather violent handling to which they are usually sub-

FIG. 7. Gross specimens of sea otter duodenum, showing appearance of perforations caused by *Porrocaecum decipiens*. These nematodes are in the earliest larval stage to be observed in sea otter—i.e., possessing a cephalic pike.

jected during capture might have a detrimental effect upon otter having numerous visceral adhesions. The disruption of adhesions at time of capture might bring about an early death in captive animals.

*Gross pathological changes.* Since sea otter apparently have little or no subcutaneous or intra-abdominal fat deposit normally, deteriorated body condition was not readily detected. A few animals were emaciated, however.

Generalized peritonitis appeared to be the eventual cause of death in case of intestinal perforation by nematodes. Upon opening the ventral abdominal wall, numerous *Porrocaecum* larvae were noted usually lying free on the surface of the greater omentum, between it and the abdominal wall. The body cavity usually contained a quantity of a thin, often blood-stained, fluid. A fibro-purulent exudate coated the serous membranes, and the intestinal coils were adherent to one another. Multiple perforations of the small intestine were the rule, although sometimes but a single perforation was noted. The omentum was usually adherent to the inflamed area. In a few cases the omentum itself was directly invaded by nematode larvae, and under

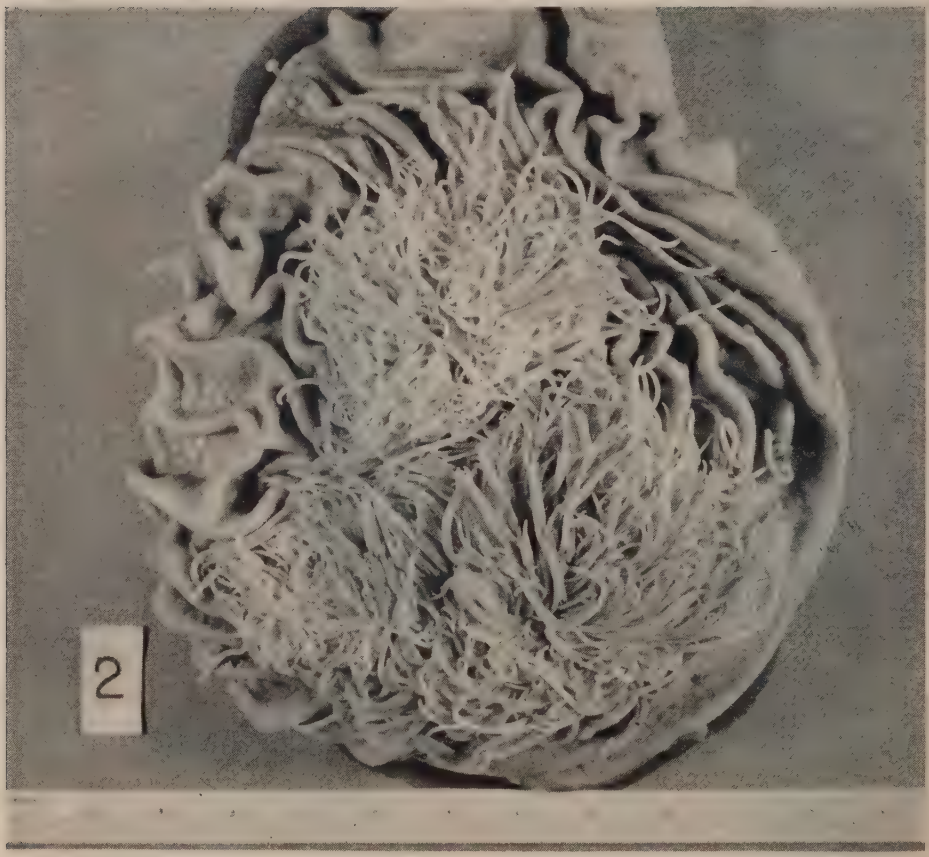


FIG. 8. Aggregations of *Porrocaecum decipiens* in stomach of sea otter. Two larval stages are represented. Tissue damage is slight.

such circumstances a thickening of the omentum was noted. Often there was further adherence to other organs—*e.g.*, spleen or liver. When such was the case, an uninterrupted way was furnished along which the larvae moved; direct invasion of spleen, liver, or other organs then resulted. Fibrosis was often advanced, resulting in very firm adhesions.

Intestinal perforations were surrounded by large inflamed areas which were greatly congested, and contrasted strongly with the normal tissue. The nematodes protruded through the perforation from the lumen of the intestine, generally in large numbers (Fig. 7). Many were deeply embedded in the tissue reaction products on the omentum, or within other organs. Incising the intestine disclosed dense aggregations of nematodes attached around the site of perforation. Such firmly anchored masses of worms no doubt occluded the intestinal lumen to a significant degree.

The body of the stomach usually showed one or more dense aggregations of nematodes, the anterior ends of which were firmly embedded in the gastric mucosa. Later larval stages predominated here, as differentiated grossly by their darker color in contrast to the more translucent appearance of the earliest stage (Fig 8). There was no evidence that the stomach wall is ever perforated.

Other organs were not characteristically affected. Any other lesions noted could be attributed to secondary effects of generalized peritonitis.

Animals with peritonitis showed a neutrophilic leukocytosis. From 26 to 43 per cent of the total leukocytes were stab cells. Eosinophiles were few or absent. From 24 to 40 per cent of the total leukocytes were lymphocytes.

*Histopathological observations.* **Stomach.** The anterior ends of the nematodes were deeply embedded in the gastric mucosa; the latter was severely eroded to the depth of the muscularis musoca in immediate area of attachment (Fig. 9). Fibrocytic proliferation was marked, and normal structure was severely altered. Cavities surrounding the nematode heads were filled with acidophilic material which probably was semifluid in the living animal. Bacilli were abundant in these cavities, particularly around the periphery of the contained substance. The nematodes penetrated usually not deeper than the muscularis mucosa, but in some cases the muscularis externa was invaded. Leukocytic infiltration was limited to cells of

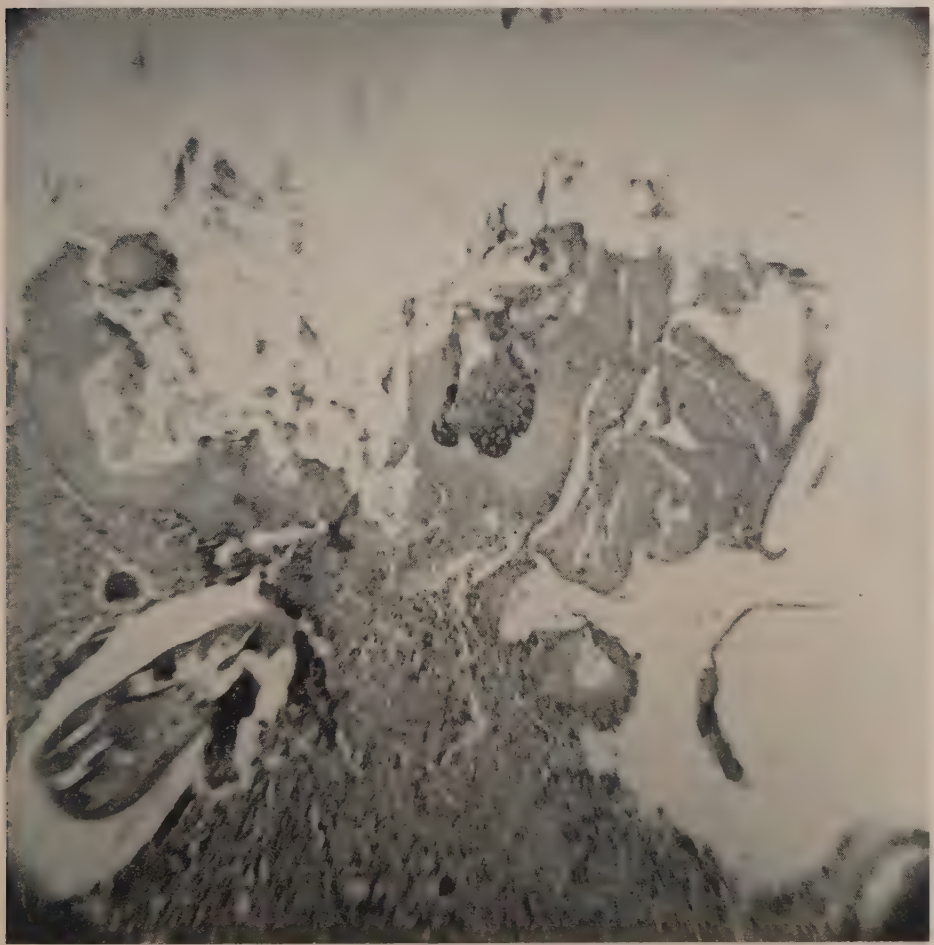

FIG. 9. Gastric mucosa of sea otter, showing injury caused by larvae of *Porrocaecum decipiens*. Low power.

a mononuclear type; polymorphonuclear cells, or their precursors, were not noted. The mucosa of the areas surrounding the sites of nematode attachment was hyperemic.

Hoeppli (1932) described the pathological changes brought about by a species of *Anisakis* in the stomach of the walrus, *Odobenus rosmarus* L. Hoeppli (1927) and Hoeppli and Feng (1931) pointed out that a degree of tissue liquefaction takes place under these circumstances, and attributed this effect to the action of the oesophageal glands. Those species infecting marine mammals appear to be particularly well adapted to this type of tissue invasion.

**Duodenum.** The areas of intestinal perforation showed fibro-purulent peritonitis. Polymorphonuclear neutrophils made up the main component of infiltrating cells. Fibroblastic proliferation was marked in the main areas of inflammation. Several nematodes protruded directly through the openings, while others were embedded at various levels in the adjacent tissue (Fig. 10). The nematodes occurred in foci, and were never observed in the intestinal wall at any distance from the invasion center. The destruction of tissue was limited also to the immediate area surrounding this focus. The surrounding mucosa showed epithelial desquamation, but seemed otherwise unaltered. Bacteria were not conspicuous except in the fragments of debris within the perforated area. Only bacilli were noted, probably coliform organisms.

**Omentum.** The serous surfaces of the omentum were in part covered with a fibro-purulent exudate; however, the serosal epithelium was often intact. Fibroblastic proliferation was marked. The cellular reaction consisted mainly of polymorphonuclear leukocytes, with good numbers of lymphocytes. Nematodes in some cases were deeply embedded in inflammatory tissue; here also was evidence of liquefaction of tissue around the anterior ends of the worms.

**Spleen.** Splenic invasion occurred only via adherent omentum. Marked fibrosis was noted. The cellular components of the exudate consisted largely of polymorphonuclear leukocytes, although macrophages were numerous. Plasma cells were also frequently observed. Hyperemia was noted in areas surrounding the nematodes.

**Other organs.** Most of the changes seen in other organs were associated with the generalized peritonitis. Amorphous casts were occasionally observed in the renal tubules.

### VII. *Corynosoma strumosum* (Rudolphi, 1802)

Acanthocephala were recorded from four sea otter. The common and widespread (both geographically and in regard to host-species occurrence) *C. strumosum* occurred in Amchitka sea otter as well as in the other marine mammals examined. A very local tissue reaction is evoked by the proboscis of the parasites.

### VIII. *Corynosoma* sp.

Among the Acanthocephala collected on Amchitka from sea otter and from Steller's sea lion was a number of specimens which represent an undescribed species of *Corynosoma*. All acanthocephalan material was turned over to Dr. H. J. Van Cleave, Department of Zoology, University of Illinois, for study. This description will be published separately.

*C. enhydris* Afanas'ev, 1941, was described from the sea otter of the Komandorskii Islands. In the opinion of Dr. Van Cleave (personal communication), the description of *C. enhydris* is inadequate. Until additional material becomes available for study, its status must remain somewhat indefinite. On the basis of proboscis hook number, however, it was determined that it is not identical with *C. strumosum* nor the undescribed species of *Corynosoma* mentioned above.

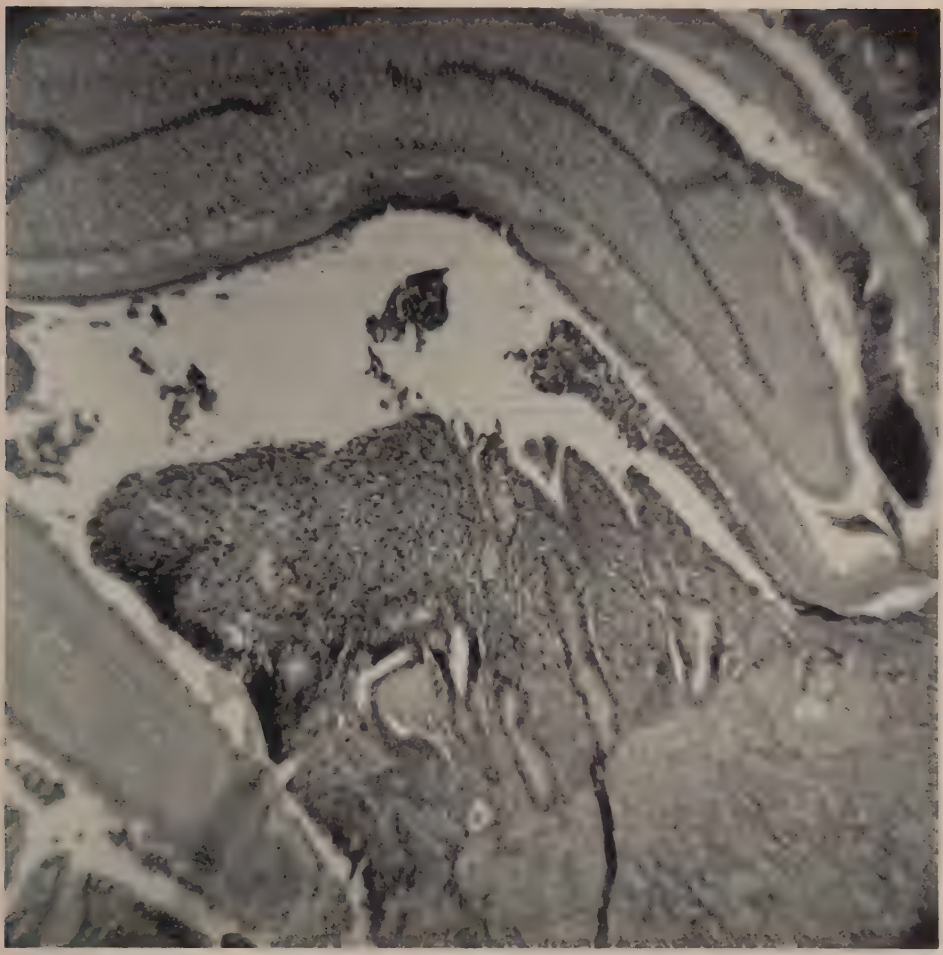

FIG. 10. Small intestine of sea otter, near perforation, showing invasion by *P. decipiens* larvae. Low power.

## IX. *Idiopathic enteritis*

Enteritis was the predominant disorder affecting sea otter during the time of this investigation. Ordinarily, it was attributable to *M. pirum* infection, but in a few instances a fatal enteritis without the concomitant trematode infection was noted.

In the absence of any recognized etiologic agent, it can only be assumed that some other factor, so far undetected, is involved. It must be emphasized also that the effect of some other disease-producing factor may be in every case superimposed upon the *M. pirum* infection, although the writer is of the opinion that *M. pirum* alone is an important pathogen. Despite these complications, this condition for the present time may be treated as a separate entity.

*Symptomatology.* In the wild state, the morbid sea otter were sluggish and relatively inactive. They seemed to frequent the beaches, where their semi-fluid, dark-colored excreta contrasted strongly with those of the normal animals. The onset of the disease was acute, and there was little physical deterioration. Greatly elevated temperatures were not recorded.

The animals continued to feed readily up to a few hours of death.

*Gross pathological changes.* A severe hyperemia of the small intestine was characteristic. Intussusception had occurred in one case, with blood stasis. As mentioned above, in reference to *M. pirum,* a tightly adherent layer of fibrinous exudate was often noted. Gastritis was ordinarily associated with the enteritis, but it was relatively mild. Petechiae were noted occasionally on the liver, and in some cases the kidneys were hyperemic, particularly in the cortical region.

*Histopathological observations.* Severe hyperemia of the villi was characteristic, with engorgement of the central vein. Peripheral hyperemia of the villi was evident (Fig. 11). The lamina propria was hyperemic, as was the muscularis externa to a lesser degree. Massive desquamation of the mucosal epithelium was characteristic, so that an important component of the exudate was mucosal fragments in which cellular identity was still preserved. Such fragments were abundant between the congested villi and the amorphous debris covering the mucosal surface. Leukocytic infiltration was lacking. Bacteria were not observed in the zone of inflammation.

The gastric mucosa was hyperemic, but epithelial desquamation was not observed. Renal hyperemia was observed in a few cases, with the congestion particularly marked in the cortex of the lobes. (The otter kidney is superficially lobed.) The glomeruli were normal.

### *Bacteriological Studies*

An effort was made to isolate any bacteria which might have been involved in sea otter enteritis. Animals near death were killed so that uncontaminated material in most favorable condition could be obtained. Inoculations were taken from all appropriate organs, and from the gastro-intestinal tract. The following media were inoculated in the field: Kligler iron agar, urea agar, plain agar, blood agar, and beef infusion broth. After incubation in the field, during which time good growth in some cases was obtained, the cultures were returned to the laboratory for study.

Non-lactose fermenting organisms as well as representative lactose fermenters were inoculated on Kligler iron agar. After incubation for 24 hours, acid and gas formation throughout the medium were considered evidence of coliform bacteria. Slants having typical acid formation with or without gas were checked with *Salmonella* and *Shigella* antisera. Organisms showing a positive reaction with the antisera were inoculated into suitable media.

*Results.* Coliform organisms predominated. In a few cases, Gram-negative anaerogenic bacilli showing some of the antigenic components of the *Shigella* group were isolated. This organism did not give the biochemical reactions of *Shigella,* however, and was possibly a paracolon. Serologically, negative results were obtained in *Polysalmonella* typing attempts. *Shigella* typing results were not significant.

If this work can be pursued further, additional investigation of the possible role of bacteria should be made. Animal inoculations and other appropriate tests should be undertaken. The possibility of involvement of other microorganisms should not be overlooked.

## Discussion

With the exception of *Microphallus pirum,* whose status is not well understood, all the helminths parasitic in the sea otter have long been known as parasites of other marine mammals. Of the helminth species discussed in the present paper, no effect to the host is recognized when *Phocitrema fusiforme* and *Pricetrema zalophi* are involved. *Pyramicocephalus phocarum,* probably a rare and unimportant parasite of the sea otter, produces localized lesions in the gastric mucosa of the bearded seal, the only host

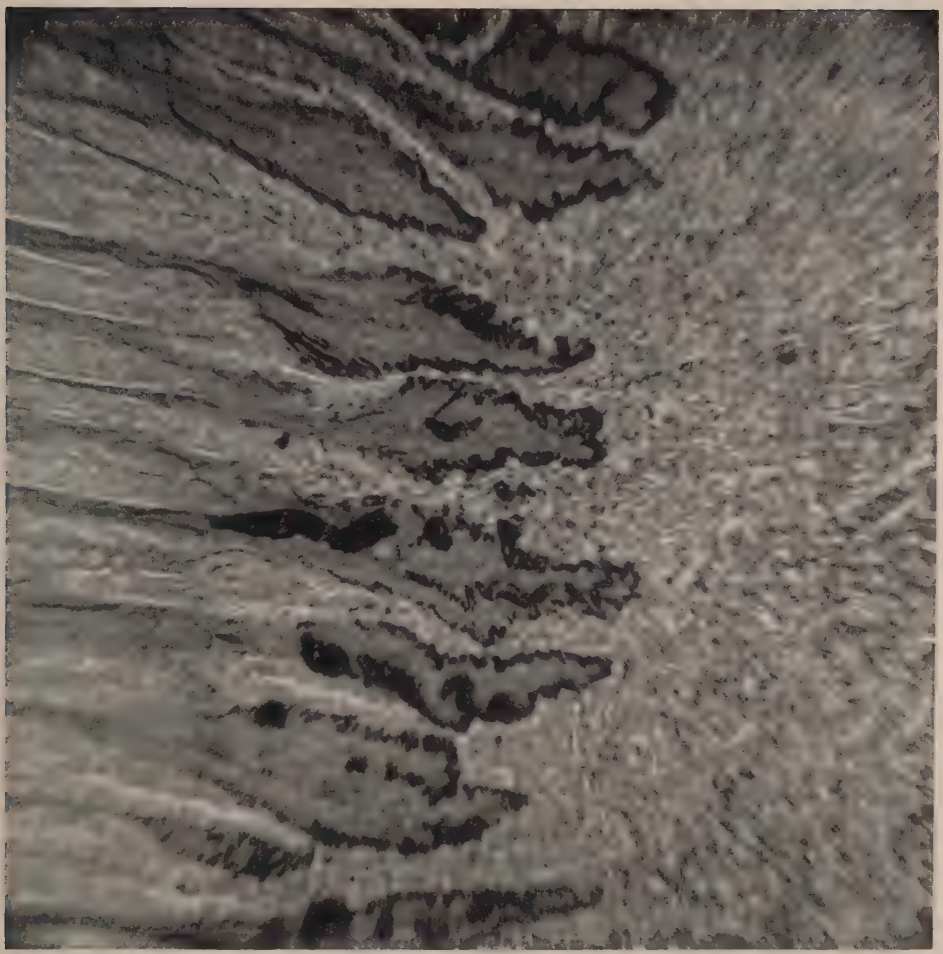

FIG. 11. Sea otter enteritis. Hyperemia of the villi. Low power.

species in which the writer has regularly observed it. The two species of *Corynosoma* reported here are unimportant parasites insofar as the sea otter is concerned. It is conceivable that the presence of great numbers of *Corynosoma* spp. might result in enough inflammation and fibrosis of the host intestine to bring about a serious effect. Generally speaking, however, the closely localized tissue reaction caused by these Acanthocephala is inadequate in amount to affect the host, at least in any recognizable manner.

*Orthosplanchnus fraterculus* parasitizes certain seals about as frequently as it does the sea otter. The writer has not observed in the gall bladder of the bearded seal (from which *O. fraterculus* was collected along the Arctic Coast of Alaska) the pathological changes regularly noted in the sea otter gall bladder. This trematode has, then, a commensal relationship with the bearded seal.

Anisakine nematodes commonly parasitize pinnipeds, and they are very abundant in Alaskan phocids [*viz.*, bearded seal; ringed seal (*P. hispida* Schreber); harbor seal]. Among otariids, the writer has had opportunity to obtain material only from Steller's sea lion. The report

by Stiles and Hassall (1899), however, gives detailed information on the occurrence of such nematodes in the Pribilof fur seal. Walrus infected by nematodes have been relatively few among those examined by the writer.

*Porrocaecum decipiens,* among others, is often seen in colony-like aggregations in the stomach of pinnipeds. A similar condition is regularly observed in the sea otter, as mentioned above (Fig. 8). In any case, the effect on the host does not appear to be important, since the amount of damage done the gastric mucosa is relatively slight.

The larval stages of *P. decipiens* and related species do not, to the writer's knowledge, invade the intestinal wall of the pinniped host. Intestinal perforation and extensive migrations in the viscera of sea otter appear to be peculiar of larval behavior in this host species alone.

The pinnipeds comprise an ancient group of highly specialized marine mammals. It is recognized that they share a common derivation with land carnivores, but the sea otter, a mustelid, cannot be considered related closely to them. It appears to the writer that the helminths considered herein, with the exception of *M. pirum,* must be regarded as having become adapted over a long period of time to a parasitic existence in pinnipeds. The sea otter, through its feeding habits, is subject to infection by helminths adapted to existence in another group of mammals phylogenetically not closely related. The attendant immuno-physiological differences may be relatively great, and unusual behavior of the helminth parasites may result.

The interrelationships of *M. pirum* are not well understood. If the hermit crab should prove to be the only intermediate-host species, the sea otter may be the only marine mammal frequently exposed to infection. Deep-water crab species should be investigated. The true role of *M. pirum* in sea otter mortality can only be elucidated through experimental work. With Schiller's finding the metacercarial stage of *M. pirum,* the establishment of experimental laboratory infections has become possible. Rausch (1947) showed that another species, *M. opacus* (Ward, 1894), is able to infect a variety of host species. A similar lack of specificity may exist in the case of *M. pirum.* The possibility that it may infect birds has not yet been eliminated. A better concept of the significance of sea otter enteritis will also come about through controlled infection experiments with *M. pirum.*

Remedial measures for the reduction of losses in Amchitka sea otter, if such are feasible, cannot be established without further investigative work. It is entirely possible that the sea otter populations here have exceeded the carrying capacity of the habitat. The present degree of consumption of hermit crabs and fishes, both of which transmit pathogenic parasites, may be an unnatural one, but one enforced through reduction of more suitable food species. Comparable studies on other islands are badly needed to determine these relationships. The significance of the unusual sex ratio among morbid otter also needs clarification in regard to that of the population as a whole.

Mr. Howard A. Powers, U. S. Geological Survey, Denver, Colorado, spent several months in 1951 on the Rat Islands, and during this time kept careful record of his observations on sea otter. According to Mr. Powers (personal communication), the relative abundance of sea urchins on the islands with fewer otter was noteworthy. Observations on the islands of Kiska, Little Kiska, and Rat Island enabled him to estimate that otter on these islands were only from 10 to 25 per cent as abundant as on Amchitka. Comparable impressions regarding the sea otter-sea urchin relationship have been expressed by others, but lack of adequate information for earlier times prevents any conclusion. This nevertheless emphasizes the need for adequate

investigation of the entire problem in the Rat Islands region.

If it is true, as stated by Barabash-Nikiforov (1935, p. 256) that the yearly increment of a sea otter population may be relatively low (only 7 per cent on Mednii Island), it is obvious that heavy losses, as suffered by the Amchitka animals in 1951, cannot be tolerated. It is worthy of mention that Mr. Powers (see above) observed only two to three dead animals on each of the islands visited by him. All appeared to have died during the winter of 1951. He made no observations on the islands of Segula and Semisopochnoi, which probably also have sea otter.

It is possible, in view of present knowledge, that the total protection afforded the sea otter in recent years (since July 7, 1911) has reached the point on Amchitka where its purpose is defeated. It does not seem unreasonable to suggest that an effort to reduce artificially the Amchitka sea otter population might be in order. The operation should be self-sustaining, in view of the relatively high value of sea otter pelts. In any event, some provision should be made to salvage the pelts of animals dying from disease, since their value is considerable, and apparently not much lessened through the disorders affecting the animals.

Effective redistribution of sea otter to other suitable habitat probably would be the most effective means to bring the species back to a numerical abundance adequate to permit some annual economic utilization. In the writer's opinion, the use of aircraft would permit the most effective removal of otter to new localities, particularly since the time spent in captivity would be greatly reduced. If the obstacles can be overcome, the potential value of the sea otter is very high.

Any attempt on Amchitka to reduce or exterminate animal species which harbor the same parasite species as the sea otter should not be considered. The sea otter-helminth relationships discussed in this paper are self-perpetuating. Destruction of seals and sea lions would not affect in any conceivable way the extent of losses among the sea otter.

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# PHOTOSYNTHESIS OF *PICEA EXCELSA* IN WINTER

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## INTRODUCTION

The reason for the common occurrence of various species of the genus *Picea* in the colder regions of the earth is still largely unknown. Work in the Bavarian Alps indicates that the local types of *Picea excelsa* Link are more resistant to low temperatures in winter than certain other native species (Ulmer 1936). Also there is good evidence that the maintenance of the leaf water content above certain levels is important during the winter when water is not readily available through the normal conductive channels (Schmidt 1936). *Picea excelsa* is apparently fairly resistant to winter drying. Other writers have suggested that early and late frosts may be of importance in determining which tree species may survive in a particular location. It is most probable that a combination of many factors determine the natural range of certain ecotypes of *Picea excelsa* and these may well include the above-mentioned factors as well as resistance to ice-break and ability to produce seed in a short growing season. Migrational and other synecological factors such as the incidence of disease may also play a role.

Another factor of considerable importance may be its photosynthetic efficiency at relatively low temperatures, both during the cool days of summer and the warm days of winter. But little or no information exists on the production of photosynthate by *Picea excelsa* during the winter. Zeller (1951) has published some interesting results on the subject but most of her work was done with annual plants that survive into the winter. None at all to our knowledge has appeared on the daily minute to minute trends of photosynthesis and respiration of this tree species in any season of the year. Since an instrument has now been perfected which can do this, the following work was carried out to determine the photosynthesis and respiration of *Picea excelsa* in the colder months.

[1] The research upon which this paper is based was carried out while the writer was at the Forstbotanisches Institut, Munich, Germany.

## METHODS

An instrument was used which measured continuously the amount of $CO_2$ in the air before and after passing over a 6 inch long twig of an intact tree in its natural habitat. Air was drawn into the sampling apparatus through plastic tubing from the tree (T) as shown in Figure 1 at the rate of 0.3 liters per min. A glass tube six inches long, one inch in diameter, and open at one end was placed over the twig and connected at the other end through a constriction to the plastic tubing. From this twig the photosynthesis measurements were obtained (Ps, Fig. 1). A similar glass tube was placed over another twig and covered with a black cloth to exclude light for the respiration measurements ($R$). A third tube with an opening two feet away from the tree was placed so as to sample the normal air ($A$) near the tree.

Air was then drawn from these three lines into the house, across the flowmeters ($F$), into the diaphragm-electric pumps ($P$), and through the silica gel driers ($D$). If the switch ($S$) was closed for a particular line, air was forced to bubble out at $B$; if the switch was open for this line, it passed into the infrared gas analyzer which determined the amount of $CO_2$ in the air (I. R. G. A.). The amount of $CO_2$ in the air in one tube ($X$) was automatically compared in the gas analyzer with the $CO_2$-free air in another

tube ($Y$). Details of the construction and operation of the instrument are given by Huber (1950) and others cited by him. The difference in $CO_2$ in the two tubes ($X$ and $Y$) was finally registered by a galvanometer which could be made to record continuously on a moving chart ($TG$). This particular recorder was synchronized to the electrically operated gas switch ($S$) so that when any one of the three air lines was open to the instrument the recorder would make a point in one of three colors on the paper chart. The timing of the point recorder was arranged so that each recording would come at the end of two minutes of passing gas through the instrument. In most cases the apparatus was allowed to run three days without attention. The only limitation to its continuous operation, if the clockwork in the point recorder had not required hand winding every three days, was the saturation of the silica gel drier with water vapor. Since water vapor, like $CO_2$, absorbs infrared light in the analyzer, a drier had to be used. About 100 ccs. of silica gel were used in each of the drying tubes, larger quantities causing appreciable lags in the recording of changes of $CO_2$ content in the lines.

At the same time, a sunlight recorder was kept on the roof of the house and a recording thermograph kept about 200 ft. away in a sheltered weather house one foot over the ground. Measurements were obtained throughout most of October and November and during the time when the snow was on the ground in early December. The tree used for sampling stood about 25 ft. high and some 30 ft. away from the recording house. The experiment was located near the village of Grafrath, some 10 miles south of Munich.

## Results

Photosynthesis of *Picea excelsa* can be very considerable in warm clear days of November and early December some time after the leaves have fallen from neighboring deciduous trees and after severe frosts have occurred. An example of a typical run during a relatively warm day in November is shown in Figure 2.

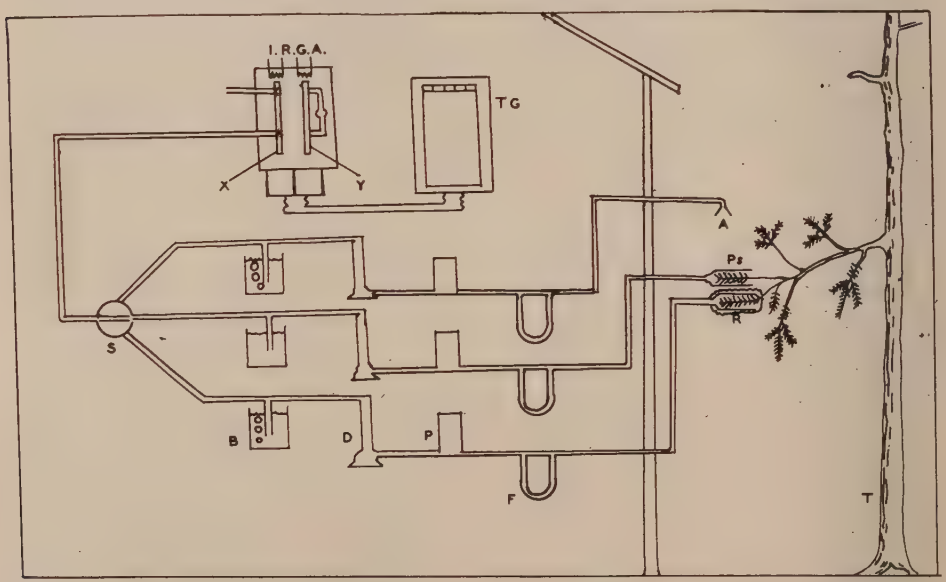


Fig. 1. Apparatus for measuring the photosynthesis and respiration of *Picea*. Explanation in text.

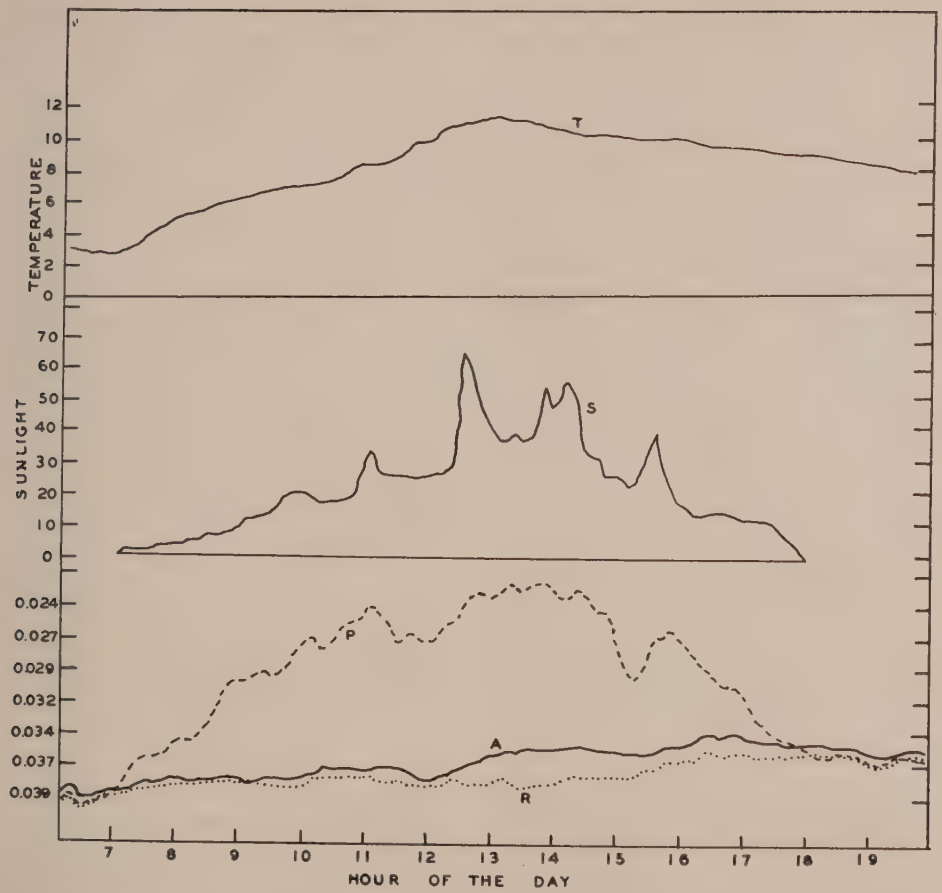


FIG. 2. Top curve: temperature in degrees centigrade ($T$); center: sunlight as a percentage of full sun ($S$); bottom: photosynthesis ($P$), normal air ($A$), and respiration ($R$) in terms of per cent $CO_2$ in the air sampled.

Photosynthesis ($P$) appears to be largely a function of the light intensity curve ($S$), but temperature can be seen to be relatively steady. Respiration is given at the same time ($R$) and it can be seen that the $CO_2$ given off by the leaves was much less than the $CO_2$ absorbed so that a certain amount of photosynthate was evidently accumulated.

On a cold day in late November when the temperature was below freezing most of the day, photosynthesis was so low as to be barely measurable (Figure 3). But at the same time respiration was so low as to be completely unmeasurable so that at these temperatures the photosynthesis-respiration balance was in favor of food accumulation. One must, of course, consider nighttime respiration, and possibly also the respiration of the rest of the plant for an accurate estimate of this balance. However, the nighttime respiration continues about the same as the daytime, depending largely on temperature.

Variations in the $CO_2$ measurements of the normal air near the tree ($A$ in Figures 2 and 3) were probably caused by changes in the $CO_2$ content of the outside air. Wind currents affected this and it was suspected that the presence of a

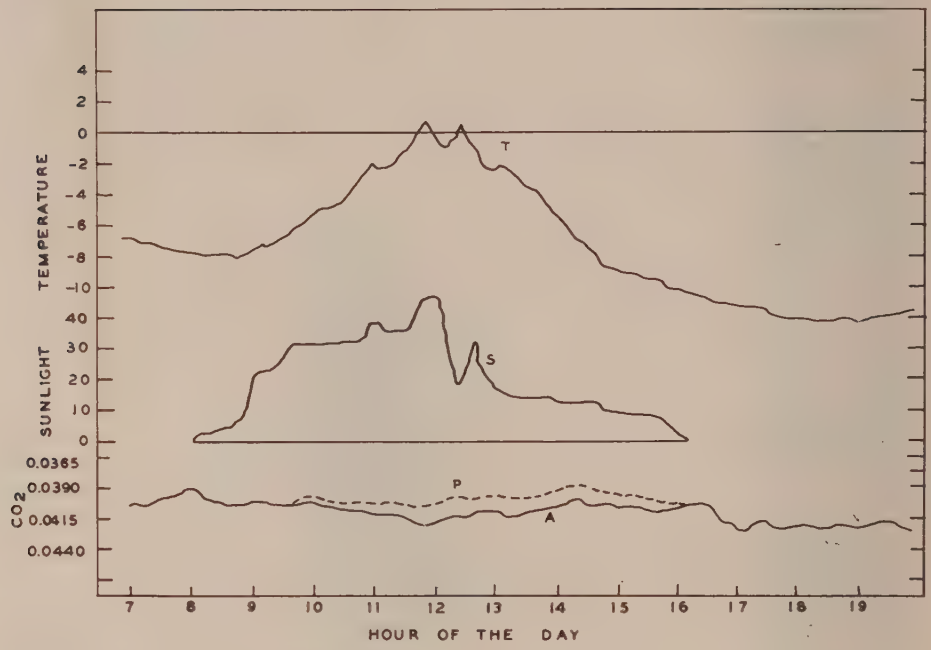


FIG. 3. Top curve: temperature in degrees centigrade ($T$); center: sunlight as a per cent of full sun ($S$); bottom: photosynthesis ($P$), normal air ($A$), and respiration (same as $A$) in terms of per cent $CO_2$ in the air sampled.

smoking chimney in the vicinity might have caused some of the variations. When the instrument was used in the city of Munich there was nearly always a climb in the $CO_2$ readings in the winter mornings as people started their fires for cooking purposes. This was especially marked on foggy days when there was little air movement. Some of the more rapid variations in the normal air curves were caused by changes in the electric power which affected the galvanometer of the gas analyzer in spite of the use of a voltage regulator.

On some of the cloudy days of November and early December rather large photosynthesis was recorded and yet very low readings on the sunlight gauge. It is possible that the light affecting the gauge is not a good measure of the light available for photosynthesis, although other factors might have entered into this anomaly, such as weather conditions previous to the time of measurement.

## DISCUSSION

These results are considered to be only preliminary. In general, it appears that photosynthesis of the Bavarian lowland strain of *Picea excelsa* may continue well into the colder months. However, it is difficult to make predictions of photosynthesis for certain climatic conditions, because as Ehlers (1915) pointed out, the weather previous to the time of measurement may affect the photosynthesis. He found that *Pinus nigra*. Arn. needles when exposed to subfreezing temperatures for several days showed no photosynthesis at 1° C., but when kept at 15° for a few days, showed some photosynthesis at 1° C. Possibly this was associated with the process of hardening which may involve a certain amount of deterioration of the chloroplasts (Schmidt 1936). It is also known that the stomatal opening is important to the photosynthesis and that low temperatures cause

a closing of the stomates. The rate of opening in a subsequent warm period varies with different species (Michaelis 1934).

Our results showed that some photosynthesis may occur when the temperature is below freezing and this agrees with the results of Zeller (1951) whose experiments extended further into the winter than our own. Zeller found that *Picea excelsa* produced some $CO_2$ at temperatures as low as —12° C. and absorbed $CO_2$ as low as —6° C. The relatively low respiration rate of *Picea* as compared to the photosynthetic rate was believed to give it an advantage over *Prunus laurocerasus* L., an evergreen native to warmer country, which had a relatively high respiration rate at low temperatures.

Unfortunately, it is difficult to compare daytime air temperatures to the photosynthesis behavior since the leaf temperature is usually a few degrees higher than the surrounding air when the sun is on the leaves. Ehlers (1915) found 2 to 10° difference between the leaves of various species of *Pinus* and the surrounding air. Michaelis (1934) suggested that there may be as much as 17° difference. It therefore appears that the temperature recorded near the tree on a thermograph is not necessarily representative of the temperature at which photosynthesis is occurring within the leaf.


## Summary

Photosynthesis and respiration of *Picea excelsa* was measured by means of a constant recording infrared gas analyzer in the late autumn and early winter near Munich, Germany. On warm, sunny days in this season photosynthesis was about four times greater than the respiration at the daytime peak. Even on cold days when the air temperature was below freezing most of the day, some photosynthate accumulation was indicated by the results. Some of the results suggested that more work is necessary before predictions can be made of the photosynthesis of *Picea excelsa* for certain weather conditions in winter.


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# AN EXPERIMENTAL STUDY OF THE INFLUENCE OF PELAGE PIGMENTATION ON METABOLIC RATE AND ITS POSSIBLE RELATIONSHIP TO BODY TEMPERATURE CONTROL AND ECOLOGICAL DISTRIBUTION

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In published studies of temperature regulation in homoiothermic animals little if any attention has been directed to pigmentation of the plumage or pelage other than as applied to protective coloration. Indeed, in arctic and tropical animals the adaptations to temperature are essentially those regulating heat conservation and loss through the fur, feathers and skin. In these animals the body-to-air temperature gradient can be adapted only by behavioral adjustments (avoidance of direct sunshine, nest building, and hibernation in a few species) as concluded by Scholander *et al.* (1950). Doubtless, insulation and the animal's ability to withstand heat or cold are of prime importance. Arctic animals are usually so well-insulated that they are protected against the extremes of cold to which they become exposed. Variability in keeping comfortable exists to some degree in the animal's posture which can affect heat loss or retention. In cases of adequate insulation by fur and fat, skin or fur color obviously would be of less importance than in those animals with only sparse pelage.

In poikilotherms, which depend upon the temperature of the environment, skin pigmentation becomes a critical factor. In studying adaptive coloration of desert lizards in relation to tolerance of high temperatures, Cole (1943) has found a tendency toward lighter-colored epithelium in those tolerating high temperatures. Atsatt (1939) has shown good correlation between color phase and the animal's need for absorption or emission of heat radiation. She observed that most of the species under study were in the light phase at high temperatures and in a dark phase at low temperatures. In animals such as the desert lizard, dependent upon external temperatures for reaching an optimum body temperature, skin pigmentation must be of prime importance.

Cowles (1941) has suggested that the light colors of nocturnal desert reptiles may aid the conservation of body heat. He suggests also (1939) that the inability of snakes to change color is a factor in their becoming crepuscular or subterranean. He is of the opinion (personal communication) that coloration is only of secondary importance in temperature adjustment but primarily for concealment. As evidence for this opinion he mentions the fact that reptiles inhabiting lava flows are jet black, even though this coloration added to that of their environment would exert a tendency toward overheating, while just a few hundred yards away the same species living on light-colored sand simulates its color.

The observations of Atsatt (1939) and Klauber (1939) indicate that pigmentation must serve an important function in temperature regulation. Cole (1943) has pointed out that climatic conditions in the majority of habitats set rigid limits to the range of possible colors which can be adopted by a species. The ideal arrangement would be one in which the animal in a cold environment like the arctic would become dark-colored during

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This work was carried on in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Purdue University.

the long period of constant light and then turn to a light color for heat retention during the long period of constant darkness. The arctic fox, ptarmigan and other forms change color in such a manner. Cott (1939) has pointed out that the arctic fox, *Alopex,* in the intensely cold northern part of its range has a white winter coat while the fox in the less intense cold of the southern part does not. That this is an inherent trait is shown by the arctic foxes in zoological gardens which regularly turn white in winter. Seevers (1938) mentions that dark-colored people have never become established in the hottest regions of the earth and that the polar bear in captivity withstands heat better than some tropical animals. Scholander, Walters *et al.* (1950) have shown that heat transfer through the fur of the polar bear increases 25 to 50 times as fast when the animal is submerged because of the complete wetting of the skin and the absence of blubber. In such an animal pigmentation of the fur would be of importance in heat loss.

To determine the extent to which hair or skin pigmentation might influence metabolism of an animal at low temperatures it was decided to compare the oxygen consumption of white mice with a similar group of white mice whose hair had been dyed black. Since a dark-colored object will absorb heat faster than a light-colored one and conversely radiate heat more rapidly, the black-dyed mice theoretically should lose body heat faster in the cold and consequently should require more oxygen to maintain their homoiothermic state.

## Material and Methods

Ten albino mice were selected for weight and sex to resemble closely ten others of the same strain which were dyed black with a commercial hair dye.* The oxygen consumption of both groups of mice was measured at different temperatures from 5 degrees to approximately 30 degrees, maintained in a constant temperature room. Oxygen consumption was measured by means of a spirometer attached to the animal chamber. In each test the animal was allowed to become adapted to the environment until the oxygen consumption became regular. All oxygen readings were converted to standard conditions and plotted graphically. The temperature of the cold room was set at progressively lower temperatures differing by approximately five degrees, which were 30, 26, 20, 14, 10-11, and 5-6 degrees C.

A second part of the procedure involved the comparison of normal black and normal white mice. Here of course strain differences are undoubtedly significant and would be were one comparing metabolism of two species. Three individuals of the C-57 Black strain and

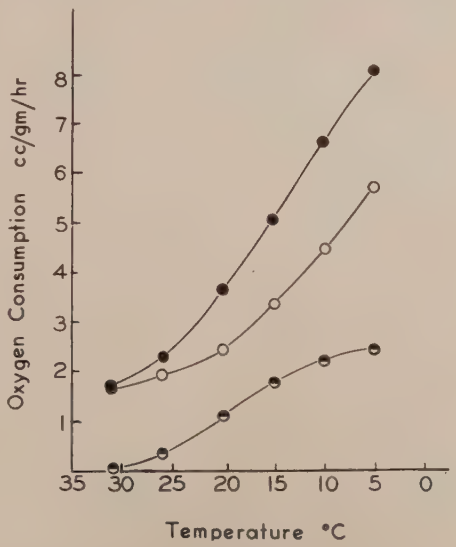


Fig. 1. Relationship of oxygen consumption of white mice, black-dyed white mice and the difference between the above two groups at different ambient temperatures of approximately 5 degree differences.

Upper line (black dots): Black-dyed white mice.

Middle line (white dots): Undyed white mice.

Bottom line (half-black dots): Difference between above 2 groups.

* Amirol, 201½ True black.

TABLE I. *Oxygen consumption of 10 white mice (W) and 10 black-dyed white mice (B) in cc/gm/hr at temperatures ranging from 5° to 32° C. All figures are averages based on 10 animals.*

| Wt. in grams | 30°-32° | 26° | 20° | 14° | 10°-11° | 5°-6° |
|---|---|---|---|---|---|---|
| 22.7±0.962* | 1.73±0.119 | 1.96±0.144 | 2.48±0.069 | 3.35±0.377 | 4.43±0.218 | 5.77±0.211 |
| 22.6±0.692 | 1.79±0.185 | 2.37±0.231 | 3.62±0.261 | 5.05±0.139 | 6.62±0.412 | 8.13±0.230 |

* $\sigma = \sqrt{\frac{\Sigma (d)^2}{n-1}}$

three albino Swiss were placed in the constant temperature room at 6-8° C. and carbon dioxide output per gram per hour was determined after one-half, 24, 48, and 72 hours.

## RESULTS

It will be seen from Table I and Figure 1 that both groups of mice used progressively more oxygen as the ambient temperature was reduced. That the oxygen uptake increase was greater with the black-dyed mice shows that black fur is definitely disadvantageous to body temperature regulation at low temperatures. At approximately 30 degrees there is little difference in oxygen consumption of black and white mice but as the ambient temperature is reduced the oxygen consumption of the black-dyed mice increases at a greater rate than does that of the white mice. At 5° C. the black-dyed mice had an average oxygen consumption which was 42 per cent greater than that of the white mice at the same temperature, and which was 467 per cent above that at 30° C. When the difference in oxygen consumption is plotted in relation to temperature, instead of a linear relationship an S-shaped curve results, indicating that the black-dyed mice had less difficulty in maintaining homoiothermy at higher temperatures than did the white ones.

The results of the second part of the experiment comparing white and normally black mice (C-57 Black) at low temperatures are given in Table II which shows a faster metabolic rate at low tem-

TABLE II. *Carbon dioxide production in cc/gm/hr of white mice (W) and black mice of the C-57 Black strain (B) at temperatures of 23°-25° C. and 6°-8° C. at periods up to 76 hours. All males. Figures are averages of 3 individuals.*

| Wt. in grams | 23°-25° | 6°-8° ½ hr. | 6°-8° 24 hrs. | 6°-8° 48 hrs. | 6°-8° 72 hrs. |
|---|---|---|---|---|---|
| 23.6±1.530* | 2.00±0.131 | 7.40±0.585 | 5.15±0.236 | 5.61±0.202 | 5.68±0.173 |
| 24.7±1.153 | 2.09±0.105 | 8.22±0.353 | 6.23±0.329 | 6.70±0.196 | 6.68±0.206 |

* $\sigma = \sqrt{\frac{\Sigma (d)^2}{n-1}}$

peratures for the normal black mice than for the whites. It also shows that some acclimatization occurred in both groups by the lower rate of carbon dioxide production at 72 hours than at 30 minutes. The oxygen consumption of the natural black mice was about one-half as great as that of the black-dyed mice which may be explained by assuming some degree of thermal adaptation in the genetically different strain of natural black mice.

## DISCUSSION

The results indicate that dark hair is disadvantageous to mice at low temperatures, for heat control is less efficient

than with white hair due to the greater heat loss. Whether the thermal advantage of white hair to an arctic animal is more important than the protective advantage of camouflage is debatable and would involve such temperature regulating aids as subcutaneous fat, vasomotor reactions, etc. Experimentally we have shown a dramatic difference in oxygen consumption at low temperatures between white and black-dyed white mice of similar strain, sex and weight. Some thermal disadvantage is seen in the black coat of the C-57 Black mouse as compared to the albino of the same species at low temperature.

## Summary

The relationship of hair pigmentation to metabolic rate in mice at different ambient temperatures was investigated by using albino mice whose hair was dyed black. Oxygen consumption was compared to that of non-dyed albino controls of the same weight, age and sex. At low temperatures the oxygen requirement of both groups increased but especially so with the dyed mice. Natural black mice of the C-57 strain were also compared with white mice, and these also showed a thermal disadvantage at low temperature but the difference was not so great as shown by the mice dyed black. Thermal attributes of pelage pigmentation are discussed.

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# NOTES AND COMMENT

## CONIFER TRANSPLANTS TO A GRASSY BALD ON ROAN MOUNTAIN

### Introduction

The presence of numerous grassy balds in the Southern Appalachians has not yet been completely explained. Cain (1930), Camp (1931), Brown (1941), and others consider them of natural origin, while Wells (1936, 1937) contends that they are of Indian origin.

Recent studies (Brown 1941) indicate that the grassy balds of Roan Mountain were once much more extensive than they are at present. As recently as a century or two ago, the total area of these grassy balds was probably 1,000 acres or more. Less than half of this area is now open grass land the remainder having been invaded by shrubs (*Alnus crispa* (Ait.) Pursh; *Rhododendron catawbiense* Michx.) and trees (*Picea rubens* Sarg.; *Abies fraseri* (Pursh) Poir.).

In the successional pattern for that portion of the summit of Roan Mountain west of Carver's Gap, it appears that rhododendron, alder, or conifers may directly invade grassy bald (Brown 1941). On an eastern slope of Roan immediately west of Carver's Gap is a heavy invasion of grassy bald directly by conifers (southern balsam and red spruce). Round Bald, immediately east of Carver's Gap, contains a grassy bald of approximately 100 acres with no trees on its summit (Fig. 1). A wedge of the coniferous forest is slowly enlarging between the hard-wood forest and the lower northwestern margin of this grassy bald. Invasion is slower here than west of Carver's Gap.

Fig. 1. Round Bald, looking east from Carver's Gap, 1937. Location of transplants indicated by arrow.

The aim of this study was to determine if conifers transplanted to the summit of Round Bald would survive and grow. It was thought that annual observations over a ten year period would indicate: (a) extent of survival, (b) rate of growth, and (c) factors affecting each.

### Methods

On the summit of Round Bald an area 16 x 16 meters was staked out. All species present were listed and frequency and coverage data recorded. This indicated typical grassy bald vegetation for Roan Mountain. A rectangular plot 8 x 16 meters, was fenced against livestock which are pastured on the mountain during summer months. A control plot, 4 x 16 meters, was left unfenced on either side of the fenced area.

In August 1937, two series of transplants were made, one consisting of individual transplants and the other of two block transplants. In October 1939, a third series of individual transplants were set.

#### *Series 1. Individual conifers*

Two hundred balsam seedlings were taken from the transition zone between forest and grassy bald, immediately across Carver's Gap, elevation 5,600 feet. Three- to five-year-old seedlings ranging from 3 to 8 inches in height were carefully dug with a pick, allowing a handful of soil to adhere to the roots of each plant. These were set 4 decimeters apart each way, 100 being set in the fenced area and 100 in the unfenced area. In like manner, 200 spruce seedlings were taken from the same area and set in fenced and unfenced plots adjacent to the balsam seedlings.

#### *Series 2. Block transplants*

To test whether soil conditions might be limiting, two block transplants were made, one for balsam and one for spruce. The blocks were taken from the same area as were the seedlings. A block of soil approximately 24″ x 36″ and 18″ deep was removed with 13 balsam seedlings intact. The seedlings ranged in height from 7 to 24 inches. This block was loaded on a sled and pulled by a mule to the site and set in a prepared pit within the fenced area. Soil was carefully tamped in around the block. The same procedure was repeated for another block containing 14 spruce seedlings ranging in height from 5 to 36 inches.

#### *Series 3*

This series of transplants was made two years later to determine the effect of prevailing winter winds on conifer seedlings. Two plots, 3 x 4 meters each, were laid out within the fenced area and each set with 80 seedlings, 40 balsam and 40 spruce. The balsam and spruce seedlings were set in alternate rows. The plot on

the eastern side was protected on the northwest with a boarded-up shield 30 inches high, while the plot to the west was left exposed.

Observations and records were made in the spring and fall of each year, except 1945 to 1948, when circumstances prevented visits to the area.

## Results

### *Series 1*

*Survival.*—Of the 100 balsam seedlings in the fenced area, 97 survived the first year, 85 the second through the seventh year, and 70 were living at the end of 12 years. Of the fenced spruce seedlings, 95 survived the first year, 78 the second year, and 75 survived the following ten years. In the unfenced balsam plot, 67 survived the first year, 20 the second year, 19 the third year, 6 the fourth through sixth years, 3 the seventh year, and only 1 survived the 12 year period. The unfenced spruce did better. Eighty survived the first year, 67 the second, third, and fourth years, 55 the fifth, 51 the sixth, 50 the seventh, and 29 were living at the end of 12 years (Fig. 2).

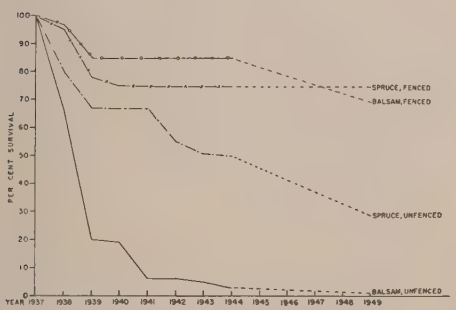
PER CENT SURVIVAL
YEAR 1937 1938 1939 1940 1941 1942 1943 1944 1945 1946 1947 1948 1949
SPRUCE, FENCED
BALSAM, FENCED
SPRUCE, UNFENCED
BALSAM, UNFENCED

Fig. 2. Survival of balsam and spruce in fenced and unfenced plots.

*Growth rate.*—The average height of seedlings at setting was recorded as 6 inches. The average height of fenced balsam seedlings the third year was 9.4 inches, 34.5 inches the seventh year, and 67 inches the twelfth year. Fenced spruce showed an average height of 9 inches the third year, 25.4 inches for the seventh year, and 68 inches for the twelfth year. Unfenced balsam averaged only 4.7 inches the third year, 10.8 the seventh year, and 24 inches the 12th year. The unfenced spruce seedlings averaged 6 inches the third year, 35.4 inches the seventh year, and 42 inches at the end of 12 years (Fig. 3).

### *Series 2*

*Survival.*—Apparently all seedlings of the block transplants survived the entire period. In the balsam block, eight additional balsam seedlings were recorded at the end of the fourth

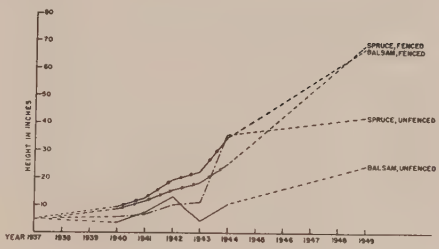
HEIGHT IN INCHES
YEAR 1937 1938 1939 1940 1941 1942 1943 1944 1945 1946 1947 1948 1949
SPRUCE, FENCED
BALSAM, FENCED
SPRUCE, UNFENCED
BALSAM, UNFENCED

Fig. 3. Growth rate of balsam and spruce seedlings in fenced and unfenced plots. Height in inches represents average height at time of measurement.

year. The eight evidently developed from seeds which were moved with the soil block. These and the original 13 were living at the end of twelve years. The 14 spruce seedlings survived the entire period. Survival was very high in both blocks. The mass growth seemed to afford some winter protection, but winter injury, especially on the side of prevailing winter wind, was noted on a number of visits (Table I.).

Table I. *Number and average heights (in inches) of conifer seedlings recorded as surviving in block transplants*

| Year | Number | | Average Height | |
|---|---|---|---|---|
| | Balsam | Spruce | Balsam | Spruce |
| 1937 | 13 | 14 | 15 | 9 |
| 1938 | 13 | 14 | .. | .. |
| 1939 | 21 | 13 | .. | .. |
| 1940 | 13* | 11* | 19 | 29 |
| 1941 | 21 | 12 | 19 | 33 |
| 1942 | 15 | 10 | 28 | 47 |
| 1943 | .. | .. | .. | .. |
| 1944 | .. | .. | .. | .. |
| 1945 | .. | .. | .. | .. |
| 1946 | .. | .. | .. | .. |
| 1947 | .. | .. | .. | .. |
| 1948 | .. | .. | .. | .. |
| 1949 | 21 | 14 | 52 | 52 |

*Obviously some seedlings considered dead, survived.

*Growth rate.*—The average height of the seedlings in the balsam block was 15 inches in 1937, 28 inches in 1942 and 52 inches in 1949. The rate of growth in the blocks was much slower than for individual settings, especially after the first three to five years. Crowding obviously slowed down growth rate (Table I.).

### *Series 3*

*Survival.*—The rate of survival for shielded balsam was 100% the first year, 94% the second and third years, and 77% for the ten year

period. In the exposed area survival was less, being 85% for the first year, 60% the second and third years, and 35% for the ten years. Survival for spruce in the shielded area was similar to that of balsam, being 100% the first year, 95% the second year, 80% the third year, and 70% for ten years. In the exposed area, 80% survived the first year, 47% the third year, which also survived the ten year period (Fig. 4).

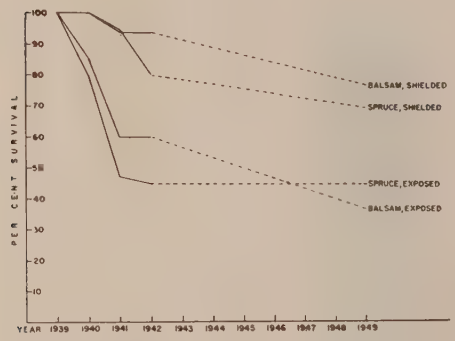


FIG. 4. Survival of balsam and spruce seedlings in shielded and exposed plots.

*Growth rate.*—In 1949, the average height of shielded balsam was 53 inches as contrasted to 36.5 inches for exposed balsam. The average height for shielded spruce was 52 inches as compared with 35 inches for exposed spruce.

## DISCUSSION

The data show that conifers can survive and grow in a grassy bald (Fig. 5). If undisturbed by man, it is reasonable to expect that they will continue to survive and grow until this experimental plot may in time serve as a "microcenter" of distribution for the area surrounding the transplants.

FIG. 5. All transplants as they appeared in 1950. Balsam transplants to left, spruce transplants center, and block transplants to right. Note survival of unfenced spruce center foreground.

It is unlikely that small balsam transplants would survive on this grassy bald unless protected from livestock, since only one of the original 100 was living at the end of twelve years. This one made less than half the growth of an average fenced balsam. Spruce would stand a better chance, since 29 of the original 100 seedlings were living after 12 years with a growth rate two-thirds that of the fenced spruce. In the fenced area grasses and sedges averaged 18 inches which was a foot taller than in the unfenced area. This protection probably aided survival of seedlings during the first two or three years.

Hoof scars and trampling by livestock caused many seedlings to die. Since spruce tolerates this injury to a greater extent than does balsam, it has a higher survival and makes better growth than balsam when both are exposed to livestock. No doubt the presence of livestock on the mountain for more than a century has retarded invasion of grassy balds by conifers, especially balsam.

Since conifers shielded from prevailing winter winds showed higher survival and better growth than exposed ones, particularly when seedlings are small, it appears that this factor lessens the chance for survival of conifers in certain areas, thus retarding conifer invasion. Winter injury in all the series, fenced and unfenced, was noted on the northwest side of most seedlings with rarely such damage on the opposite side. The heavier formation of glaze on the side facing prevailing winds accounted for many broken twigs. Perhaps ice-storm injury played its role in retarding growth, especially on the windward side.

There remains the question of why conifers have not invaded this bald. The data indicate that the site is not unfavorable to growth and survival of conifers once they become established. The seedlings set out directly in the site compared favorably to those of the block transplants. Consequently, the black loam (20-26 inches deep), of a type formed under grass cover, cannot be a factor in growth and survival. Likewise, winter injury does not appear to inhibit seedling growth sufficiently to be a limiting factor.

Apparently, reasons for the absence of conifer invaders on Round Bald must be sought in the earliest phases of establishment. If an adequate supply of seeds is carried to the bald, it may be that their germination is somehow inhibited or that, assuming germination, the very young seedlings do not survive. The supply of seeds may be low because prevailing winds on Round Bald do not come over a nearby stand of conifers. Again, mice and the red squirrel (boomer), common seed-transporting rodents of the spruce-fir forest, are not seen on the bald. The extent to which birds may carry in seeds is unknown.

Whatever the supply of seeds on the bald, their germination and the survival of young

seedlings must be inhibited because some 2000 feet northwest of the site is a definite invasion of the grassy bald by conifers. Here, for a distance of 100 feet out from the margin of young forest, there are scattered seedlings, many of which survive. As each comes to maturity, it serves as a parent or "micro-center" of distribution, thus producing the "hen-and-chickens" pattern of invasion so conspicuous on several parts of Roan Mountain (see Brown 1941: Fig. 29). As the "chickens," or second generation trees, become more numerous or larger, secondary invasion appears to be in mass. If this trend continues here, even though restricted to the margin of forest, it is not improbable that Round Bald will eventually be covered with spruce-fir forest.


### Summary

1. In August, 1937, 200 balsam seedlings and 200 spruce seedlings were transplanted to the summit of a grassy bald on Roan Mountain to determine extent of survival and rate of growth. Half of the transplants were fenced and half not fenced in order to determine the effect of livestock upon survival and growth. A block of balsam and one of spruce were transplanted to the fenced area to determine if soil was the limiting factor in survival of conifers.
2. In October, 1939, 80 balsam seedlings and 80 spruce seedlings were set within the fenced area, half of which were shielded from prevailing winter winds and the other half exposed to them, in order to determine the effect of such winds upon survival and growth.
3. Survival was greatest for seedlings of the block transplants. Survival and growth of individual seedlings was much higher in fenced areas than in unfenced areas. Spruce showed more tolerance to livestock than did balsam.
4. Survival and growth was decidedly higher for transplanted conifers shielded from prevailing winter winds than for those exposed to such winds.
5. The data indicate that conditions on Round Bald are favorable for the growth and survival of transplanted seedlings of spruce and, to only a slightly lesser extent, for fir. Explanation for the absence of natural seedlings must therefore be sought in the seed supply or in factors which may inhibit germination and early establishment.
6. Under apparently similar circumstances, but along the margin of young forest nearby, seedlings do become established and the forest is advancing into the bald in such a fashion that ultimate natural forestation of the entire bald is not improbable.


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## FLUCTUATIONS OF SOME ILLINOIS FOX POPULATIONS

In Illinois, bounties are paid on certain animals by the county governments. The state government allocates no funds whatsoever for this purpose. However, the state legislature has "An Act authorizing counties to allow a bounty on fox scalps. Approved July 9, 1943, Chap. 8, Sec. 122a, Par. 1, *et seq.* Smith-Hurd Revised Statute, 1949." Although this act refers specifically to fox scalps, there seems to be no statute preventing a bounty on other animals which are not protected by restrictions of the Illinois Game Code.

A data sheet was mailed to each of the 102 county clerks in Illinois. This data sheet, properly filled out, would contain the number of animals bountied (fox, wolf, groundhog, and other; a separate column provided for each category) and the amount of bounty per animal for each of the years 1940 to 1950 inclusive.

During the years 1950 and 1951 the writer visited 72 of these counties and spoke to various residents, thereby gaining information about the fauna of the areas. In some instances, published reports in newspapers by the County Clerk offices have provided additional information.

Fifty-two sheets were returned. Of these, two contained no report (Whiteside and Kane Counties), and one (Peoria) contained an incomplete report. Fourteen of the counties which reported did not pay bounties of any kind during the ten year period. Only one county (Lee) paid bounties on foxes (*Vulpes fulva* and *Urocyon cyonargenteus*) throughout the entire period from 1940 to 1950. Boone County has paid fox bounties since 1942.

Both Lee and Boone Counties are in the northern section of the state. Lee County is approximately two and a half times the area of Boone County.

Until 1945 Boone County had paid $2.50 for all fox bounties. Since that time this county paid $2.50 for fox cubs and $5.00 for adult foxes with the exception of 1947 when $10.00 was paid for each adult fox bountied. Lee County paid $3.50 for foxes bountied through 1941 and $5.00 for each fox bountied since 1941. Bearing in mind that 1947 ($10.00) and 1948 (back to $5.00) were unusual years for Boone County there is a very striking similarity between the two counties in comparative numbers of bountied foxes per year. (Fig. 1).

FIGURE 1

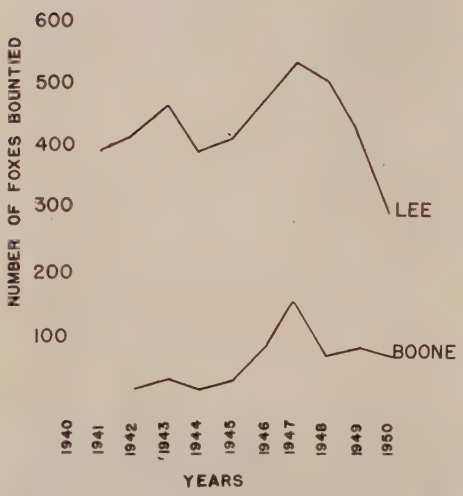


FIG. 1. Lee County paid $3.50/head (1941-1942) and $5/head (1943-1950). Boone County paid $2.50/head (1942-1944), $5/head (1945), $5/adult and $2.50/pup (1946), $10/adult and $2.50/pup (1947) and $5/adult and $2.50/pup (1948-1950).

Note the exaggerated increase in 1947 in Boone County and the extreme 1948 drop. Both the increase and drop were probably caused by the sudden changes in the amount of bounty payment.

Carroll and Adams Counties are nearly equal in area. Lake County is slightly smaller than either Carroll or Adams. In addition, Lake is suburban to Chicago and hence heavily populated while Carroll and Adams Counties are more extensively cultivated than is Lake. These factors (smaller area, heavy population, and little cultivation) have very likely contributed to the fact that Lake County has had fewer bounties than Carroll or Adams Counties (Fig. 2).

FIGURE 2

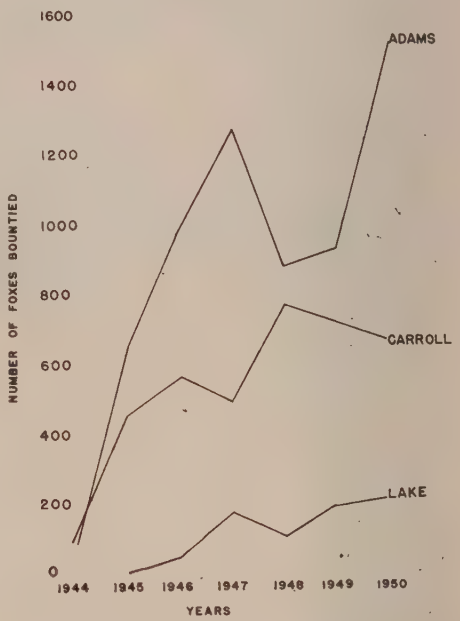


FIG. 2. Adams County paid $2/head (1944-46), $2/adult and $1/pup (1947), $1/head (1948), $2/adult and $1/pup (1949) and $2/head (1950). Carroll County paid $2.50/head (1944-1947) and $5/head (1948-1950). Lake County paid $5/head (1945-1950).

Adams and Lake counties are exceptional in not showing a decline of fox bounties in 1949 and 1950. Carroll County is exceptional in showing a 1947 decline and a 1948 peak.

## DISCUSSION

According to Mohr (1947) red fox populations were greatest in Massac and Rock Island Counties in 1947 and lowest in 1937. Jo Daviess County was apparently at its highest fox population in 1947 and at its lowest in 1932. Adams and Mason Counties had also increased to a high in 1947 (Mohr 1947).

The report for Adams County (other coun-

ties mentioned by Mohr did not report in the present investigation) shows a definite peak in 1947 with a drop during 1948 and 1949 and a sharp rise in 1950 (Fig. 2). Data from additional counties also indicates a rise in foxes bountied for 1947 (Fig. 2).

Haller (1951) indicates highs for foxes in northern Indiana in 1926, 1934, and 1946. In southern Indiana the high was reached in 1948-1949 (Haller 1951). There is a decrease in the Indiana fox population since 1949 in most of the counties (Haller 1951). Indiana and Illinois have similar bounty systems.

According to Brown and Yeager (1943) there was an upward trend in the fox population from 1938 to 1943. Mohr (1943, 1947) agrees with this. Bounty data for Lee and Boone Counties also indicate a steady rise to 1943 (Fig. 1). Unfortunately, the only data available for all the years between 1943 and 1947 in Illinois are for Lee and Boone Counties. No published reports are known to the writer for these years. However, since the data for these last-mentioned counties seem to substantiate the findings of other investigators as to the population trends of foxes in the aforementioned periods, it appears that the data from 1943 to 1947 in this report may be indicative of the true condition prevailing during that period.

Summary

There was a rise in the number of foxes bountied each year until 1943, with a drop for 1944 and a steady rise from 1944 until the peak of 1947 (Fig. 1). This indicates a major peak in fox populations preceded by a minor increase with the latter being followed by a slight decline. It would be interesting to know whether or not this were actually the case.

In most instances it appears from the available data that a decline in Illinois fox populations began in 1948 or 1949 and is still continuing (Fig. 1, Fig. 2, and Haller, 1951). Data concerning "wolves" and groundhogs were insufficient for tabulation.

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## ECOLOGICAL LIFE CYCLE OF SEED PLANTS[1]

Comparative studies of the life cycles of plants have most frequently been made from the strictly morphological point of view. Attempts to examine the life cycle from the vantage points of other botanical disciplines such as physiology or ecology are much less frequent, and successful attempts to integrate all aspects of our present knowledge of plant life cycles into a single account seem to be nonexistent. Until a more complete accounting of life cycles from the specialized disciplines has been accomplished, a thorough integration will, of necessity, probably not be realized.

Many of the ecological aspects of life cycles are of considerable theoretical and practical interest. Although the literature on some of the important ecological phases is voluminous, many problems which appear to be equally important have not received their due share of attention. It would seem that a survey of ecological aspects of all life cycle stages might help in detecting those problems which are in relatively greatest need of investigation. It is hoped that by pointing out some of the more vital ecological questions, along with listing review articles and representative studies, the following discussion may be of use to those who might be persuaded to undertake investigations of ecological life histories or certain aspects thereof.

For convenience, the general outline presented in Figure 1 will be followed. Each of the stages named in the figure can be defined for a given species so that they do not overlap appreciably in time, and hence can be discussed in sequence.

First, two problems relating to the life cycle as a whole deserve attention, although the solution of both is based on an understanding of each individual stage of the life cycle. One question is that of deciding what process or

[1]Based on a paper read at the symposium, THE LIFE CYCLE OF THE ANGIOSPERM, before a joint session of the Botanical Society of America and the Ecological Society of America at Ithaca, New York, September 10, 1952.

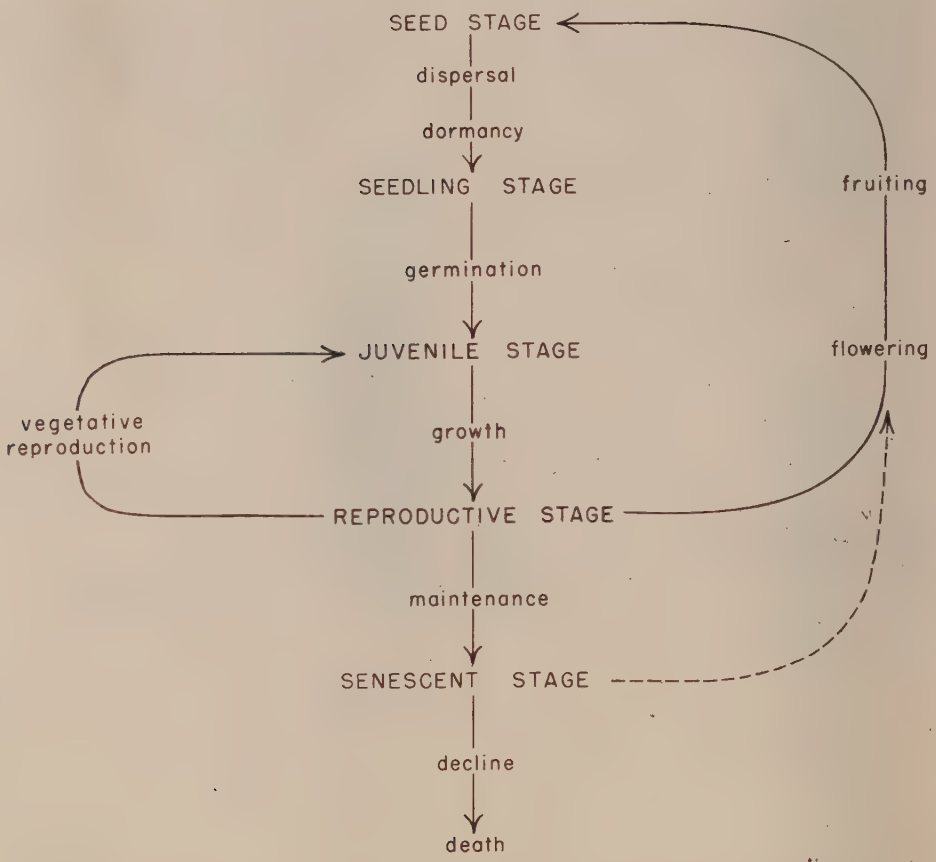


FIG. 1. Generalized diagram of the ecological life cycle of a seed plant. The dotted line suggests the heavy flowering and fruiting which senescent plants sometimes experience.

stage of development is ecologically, that is from the standpoint of survival, the most critical in the life cycle. There is general agreement that the critical stages are usually to be found during reproduction and the early stages of development (Phillips 1927; Weaver and Clements 1938: 140-143; Cain 1944: 9; Turrill 1948: 145; Baker 1950: 247; for specific work see discussion of each stage below). Although the establishment of the young plant following germination is perhaps usually found to be the most crucial single period, each situation is a separate case and precludes broad generalizations. For both theoretical and practical reasons there is need for the study of specific life histories of plants of various life forms and habitats in order to evaluate each process and stage of development from the standpoint of adaptation and survival.

Another problem relating to the life cycle as a whole, one which has occasioned controversy since the early work of Klebs, is that of the relative importance of internal versus environmental factors in determining the course of the life cycle stages, such as growth and flowering. This question, as well as other work on the physiology of development in plants, is currently receiving a great deal of deserved attention, as described in the thorough review by Whyte (1946). Yet there have been so-far few attempts to evaluate the significance of such phenomena as photoperiodism, thermoperiodism, and vernalization for other than crop plants, and their role in determining the distribution and abundance of plants under natural conditions is not at all clear. Attempts along this line are described under the Reproductive Stage below.

### SEED STAGE

Considering now some special problems relating to particular stages of the life cycle we

may logically start with the seed. With a few exceptions this is the most mobile phase of the life cycle of seed plants, and therefore some problems centering around dispersal may appropriately be discussed. The unsolved problems are seldom even implied in the oversimplified generalizations of dispersal mechanisms to be found in textbooks. For example much observational and especially experimental data are still needed in order to determine the absolute and relative effectiveness of assumed dispersal adaptations. Reviews of the scattered and isolated studies which have already been made in this direction may be found in the works of Ridley (1930) and Wulff (1943: 115-136) (*cf* Baldwin 1942: 24-26; Cain 1944: 154-161; Baker 1950: 208-217; Turrill 1951). In comparing dispersal adaptations of different plants the possibility should be kept in mind, as pointed out by Good (1947: 262-263), that beyond a certain limit an increase in dispersal efficiency may lead to definite disadvantages to the species through excessive waste of disseminules. This possibility has apparently been accorded little recognition by those interested in dispersal.

A related question, of particular interest to plant geographers, is the possibility of long distance, or saltatory, dispersal. As has been repeatedly emphasized by various writers, such as Wulff (p 128), Cain (pp 155-156), and Turrill (1951), there is very little concrete information upon which to base any sound judgment of whether or not long distance dispersal in one jump is of real importance. The weight of opinion currently seems to discount the importance of such events in causing widely discontinuous distributions of plants (see Wulff, pp 115-136; Cain, pp 283-285), although as Turrill has said (1951), ". . . the problem is no more solved than it was in the time of J. D. Hooker and other early phytogeographers." The most realistic working hypothesis seems to be that which allows long distance dispersal as one of several methods by which disjunct distributions are attained, as has been admirably outlined by Stebbins (1950: 343-345). Accepting this hypothesis, however, means that much observational and experimental work must be done on each group with a discontinuous distribution in order to determine the probabilities of long distance dispersal, and what is even more crucial, the chances of establishment in the new area. Detailed life history studies in these critical groups would seem to be a desirable and even necessary procedure if these distributional problems are to be much clarified.

Of vital importance in the study of any phase of seed ecology is the evaluation of mortality at this stage of the life cycle. Before, during, and after dispersal, seeds are subject to much loss and injury. From studies of forest trees, such as the classic work of Watt on oak (1919) and beech (1923), the most important destructive agents of seeds, sometimes controlling the abundance of the species, appear to be rodents and birds, but the few studies which have been made do not permit valid generalizations (see review by Baker 1950: 218-227). The natural longevity of seeds which survive animal destruction, and yet which do not meet conditions favorable for their germination, is not well-known. Although numerous studies of seed longevity have been made (reviewed by Baldwin 1942: 82-94; Crocker 1948: 28-66), only a few of these have been related to natural conditions of storage on or in the soil. Longevity of seeds under partial vacuum or in a refrigerator would be expected to be very different from longevity under natural storage on the plant or in the soil.

Ecological aspects of seed dormancy offer a promising field (Baldwin 1942: 110-118; Crocker 1948: 67-138). Correlations of the type and depth of seed dormancy with the life form and habitat of the plant and with the place of natural storage need investigation similar to that of Nichols (1934) on cold requirements of seeds in relation to distribution, of Mirov (1936) on correlations between type of dormancy, altitudinal distribution, and life form, of Beadle (1952) on seed dormancy of saltbushes in relation to their habitat, and of Stone and Juhren (1951) on the relation of brush fires to seed viability and dormancy of chaparral plants. Quantitative data on the significance of other seed characteristics to habitat, abundance, or life form have been obtained only occasionally, such as that for seed size and weight by Salisbury (1942), resistance to prolonged submersion by Toumey and Durland (1923), endurance of desiccation by Korstian (1927), and resistance to bird and mammal digestion by Krefting and Roe (1949).

### Seedling Stage

The seedling stage may be considered as that short period in the life cycle between the emergence of the radicle from the seed coats to the exhaustion of the food reserve of the seed, accompanied by the establishment of the normal nutritional pattern of the species (*i.e.*, autotrophic or heterotrophic; presence or absence of mycorrhizal fungi or nitrogen-fixing bacteria). The seedling stage is frequently considered to include also the so-called "period of establishment" which is here being deferred to the next or juvenile phase (Baker 1950: 247).

A great deal of information is available on the requirements and tolerances of germination under laboratory conditions for temperature, moisture, oxygen, light or darkness, or various chemicals (Baldwin 1942: 103-134; Crocker

1948: 67-138; Crocker and Barton 1953). Little attention, however, has been given to correlating these requirements with survival and distribution in nature. More germination studies are needed in which both laboratory and field work are performed, such as those of Watt (1919; 1923), Korstian (1927), Fivaz (1931), Gemmer, *et al.* (1940), Went (1948; 1949), and others mentioned in the preceding and following sections or reviewed by Baker (1950: 228-245).

A very general and significant problem in the life cycle of seed plants relates to the development of the normal nutritional pattern in the seedling stage or shortly thereafter. The main interest here has been concentrated in the past on anomolous groups such as parasites and colorless saprophytes. Yet, as Kelley (1950) has emphasized in his recent review, we are far from elucidating the symbiotic relations which the great majority of green vascular plants appear to exhibit with fungi. An understanding of the ecological life histories and the factors affecting the distribution of seed plants can never be complete without a knowledge of the role played by symbiotic as well as by parasitic fungi.

### Juvenile Stage

The juvenile stage of development can be defined as that period following independence of the food reserve in the seed but preceding vegetative or seed reproduction. This stage is frequently considered to be the most critical phase of the life cycle. Most detailed studies of mortality of juvenile stages of seed plants in nature have been made on conifers, the work in North America being reviewed by Baker (1950: 247-280). Those on angiosperms include work on oaks (Watt 1919; Wood 1938), beech (Watt 1923), birch (Linteau 1948), mesquite (Paulson 1950), a subalpine grass (Ellison 1949), desert perennials (Shreve 1917), and various prairie and woodland plants (Clements and Weaver 1924; Clements, Weaver, and Hanson 1929; Blake 1935). Survival studies which are carried out under the more controlled conditions of the greenhouse, such as those on *Atriplex* (Beadle 1952) and several grasses (Glendening 1941; Olmsted 1942; Mueller and Weaver 1942) are very useful in interpreting and predicting results in the field. Such investigations, however, are most desirable when combined with equally intensive field work.

The relative development of above and below ground parts from germination to maturity has been only occasionally studied outside of a greenhouse, and even more rarely under undisturbed natural conditions. As examples of work along this line might be mentioned that on lodgepole pine (Preston 1942), on several hardwoods (Holch 1931; Biswell 1935), on guayule (Muller 1946), on a number of prairie plants (Clements, Weaver, and Hanson 1929), and on some common weeds (Frazier 1943). Correlations of juvenile root habits of a number of tree species with their soil tolerances have been shown by Toumey (1926), but additional work of this kind is needed.

It would seem reasonable to suppose that close studies of natural mortality in seedling and juvenile plants would help clarify certain problems concerned with the operation of natural selection. In particular, the relative importance of juvenile compared to mature stages in natural selection is not yet agreed upon, as shown in the controversy of some years ago between Salisbury (1930) and Fisher (1930) (*cf.* Salisbury 1936; Salisbury, *et al.* 1933; Huxley 1942: 467-468). Furthermore, the actual effectiveness of natural selection in the juvenile stages of plant life cycles has itself been strongly questioned even in the last decade or two by writers such as Watson (1936) and especially McAtee (1937). Detailed field investigations of juvenile mortality in relation to natural selection would definitely seem to be in order if these matters are to be more clearly understood.

A technique which is currently receiving considerable attention is that of studying adaptation and evolution by comparing the environmental responses of various ecotypes of a single species under conditions which approach those in nature. Many of these studies have been made by using established transplants, but ecotypic differences which are expressed in earlier life cycle stages, such as those of the seedling or juvenile, must be critically important in survival. Examples of studies which do compare seedling and juvenile ecotypes as well as mature plants under field conditions are mentioned by Baldwin (1942: 36-39).

### Reproductive Stage

Most autecological studies have been made on mature plants of reproductive age, and interpretations of adaptation and distribution are frequently based almost entirely on this one stage of the life cycle. Since the bulk of the literature in physiological ecology is concerned with the mature stage, no attempt will be made to review the recent developments here (for reviews of the literature see Lundegårdh 1931; Weaver and Clements 1938; Daubenmire 1949). From a life history standpoint, much more pertinent is a *comparison* of the environmental response and adaptation of all stages of development in the endeavor to discover what environmental factors are limiting and upon what life cycle stages these factors exert their determining effects. An excellent example of how this may be done from a physiological

point of view may be found in the writings of Chapman (1942) on halophytes.

Although not an invariable rule, the individual plant tends to become progressively more and more secure as it approaches reproductive age. Considering first the ecology of natural reproduction by vegetative organs, such as rhizomes, runners, and aerial bublets, we find a sadly neglected field. This is true in spite of the wide-spread occurrence and importance of the many types of reproduction falling into the vegetative category (agamospermy is here considered to be genetically, but not ecologically, a type of vegetative reproduction). Few quantitative data are available concerning the relative reproductive and dispersal efficiencies of different organs of vegetative reproduction. The same is true of the ecological importance of vegetative compared to seed reproduction and dispersal in plants of different life forms and habitats. A great many more investigations like that of Mueller (1941) on the ecology of rhizomes are needed. Some of the few generalizations on this topic have been presented in the writings of Salisbury (1929; 1942) (*cf.* Ridley 1930; Coulter, Barnes, and Cowles 1931).

The production of seeds involves a complex series of processes and organs, all of which are extremely sensitive to environmental influences. As implied above in connection with the physiology of development, the intimate relation of flower bud initiation to environment, particularly day length and temperature, is currently being intensively investigated (reviewed by Whyte 1945). Since most attention has been placed upon highly modified crop plants, only some of the work on flower initiation, such as that on side-oats grama (Olmsted 1944; 1945), on desert annuals (Lewis and Went 1945), on bluestem (Curtis 1950), and on *Brodiaea* (Stone 1951) (*cf.* Baldwin 1942: 5, 12-18), have as yet been related to plants growing under natural conditions.

A field in which there has been much worthwhile observational and some experimental study is that of flower pollination. Among the needs here are the critical testing of long assumed adaptations favoring pollen transfer by some particular animal or physical agent, mechanisms favoring cross or self pollination, and adaptations protecting pollen and nectar from rain or non-pollinating animals. Furthermore, little is known of the relations of particular floral characteristics to habitat and climate, or to the life form, distribution, and abundance of the plant. Few advances have been made in understanding these problems since the classic labors of Müller (1883), Kerner (1895), and Knuth (1906-09) (*cf.* Clements and Long 1923; Coulter, Barnes, and Cowles 1931: 332-391; Weaver and Clements 1938: 256-267). Stebbins (1950: 503-510; 1951) and Grant (1950) have recently presented some interesting hypotheses on the ecological significance of certain floral characteristics normally thought of as neutral in selective value, but these, along with many earlier described floral adaptations, need additional evidence before complete acceptance.

The ecology of pollen is poorly understood. As has been emphasized by Holman and Brubaker (1926), much more work is necessary if we are to demonstrate any convincing relationships of pollen production, viability, and longevity with pollinating agent, climate, habitat, or life form. Production and mortality of flowers and pollen under natural conditions, as well as of fruits, seeds, and seedlings, are in need of comparative studies like those of Phillips (1926; 1927).

Following fertilization, the developing fruit is subject to the action of the environment for a relatively long period of time, during which its chances of surviving are often small (Phillips 1927; Baker 1950: 188-190). Potential seed production is a characteristic of plants which is of significant survival value for this as well as for other reasons. Some time ago Salisbury (1929), remarking on our state of knowledge concerning seed production of native plants, stated that, "Despite their obvious importance there are unfortunately surprisingly few available data respecting the vital statistics of plants, and the desirability of remedying this deficiency cannot be overemphasized." Salisbury later (1942) made an excellent contribution towards filling in this gap in our knowledge, but only a few studies of camparative seed production of native plants of various life forms, habitats, and abundance are available in this country (see Stevens 1932; Downs and McQuilkin 1944; and reviews by Baldwin 1942: 12-24, and Baker 1950: 182-195). In 1916, Clements wrote (p 65), "It is probably that the quantitative investigation of the seed production of dominant and characteristic species will go far towards revealing the real nature of dominance." Notwithstanding the need for this type of work, Clement's statement is perhaps somewhat over-optimistic, for as Turrill has said (1948: 180), "Average reproductive capacity gives an incomplete picture without some knowledge of its translation into reproductive actuality in natural survival of viable seeds, their germination, and the establishment of the seedlings." Terrill is here calling for the extension of quantitative studies of the life cycle throughout the period of reproduction and establishment. It seems to the writer that this type of work needs to be extended even further, to cover the entire natural life cycle of plants from the seed through senescence.

The relative importance of inherent and environmental factors in causing periodicity in

fruiting of many woody plants, as well as the survival value of this characteristic, are of considerable ecological and practical interest (see preceding citations). In addition, the important relations between viability, size, and dormancy of seed and the age and vigor of the plant producing it have been only touched upon by a very few researches, such as those of Salisbury (1942) (*cf.* review by Baldwin 1942: 32-33, 109-110).

### Senescent Stage

The senescent stage can at best be defined only vaguely, but might include that terminal portion of the life cycle in which growth and usually reproduction are greatly diminished. In a thorough review by Crocker (1942), it was concluded from somewhat conflicting evidence that plant meristems themselves probably do not become truly senescent, although they may appear to do so as a result of the accumulation of viruses. Disregarding this question, there is strong evidence that trees at least do become senescent, even though their meristems remain potentially vigorous, because of increasing difficulty in water conduction, decreasing efficiency of surface soil utilization by roots, a smaller ratio of photosynthetic to non-photosynthetic cells, and other features (Baker 1934: 153-155). These conditions, however, are probably never in themselves a cause of death, but act by increasing susceptibility to external agencies, particularly heart-rot organisms and wind. In monocarpic plants senescence is closely dependent upon factors which induce flowering, since the individual dies following fruit production. Although many data on longevity in plants have been compiled by Molisch (1938), we actually know very little of the average and maximum life span of plants in nature. New techniques are necessary for the determination of ages of plants which do not have definite annual growth rings. Possibilities along this line are illustrated in the age estimations of cacti by Shreve (1910), of ocotillo by Darrow (1943), and of several perennial forest herbs by Whitford (1951). Even in trees in which the ages can be fairly accurately determined little is as yet known of the relation between longevity and habitat, or of the changes in growth, reproduction, and response with increasing age (for some generalizations see Baker 1934: 155). The curious cases of certain monocarpic bamboos which flower simultaneously and then die over large areas at regular intervals of several decades is an interesting problem which has yet to be solved (Seifriz 1920).

### Conclusions

At least two types of approaches to a study of the ecological life histories of plants might well be stressed. The first of these is the approach which has been emphasized above, in which particular stages or processes of the life cycle, such as seed dispersal or pollination, are investigated in detail, frequently on a comparative basis for a number of species or life forms. The second type of approach is that of following the entire course of the life cycle of individuals of a given species or population, and describing and evaluating the environmental requirements, the adaptations, and relative mortality of each stage of development, using quantitative methods wherever practicable. If this were done systematically for each important species (or genus), even if on a relatively descriptive and comparative level, it would be of great value in furthering the development of a truly "Biological Flora of North America," much as that which is now underway in the British Isles (see review by Richards 1945). This procedure was first seriously considered for this country by Lawrence (1948) (*cf.* Ganong 1907; Lawrence 1949, 1950; Fitch 1951; Lindsey 1952), and outlines and bibliographies for life history surveys of vascular plants are currently being published by the Ecological Society of America (Pelton 1951; Penfound 1952; Stevens and Rock 1952; Curtis 1952).

The importance of autecological information of this type to the applied plant sciences, especially forestry, range management, soil conservation, and weed control, has been emphasized by a number of workers (Sampson 1917: 56-57; Phillips 1927; Olmsted 1941; Koroleff 1944; Duncan 1952). The role of autecology in plant sociological or vegetational studies has been recognized by numerous investigators and seems to be gaining increasing attention (Clements and Weaver 1924; Tansley 1946: 138-143; Oosting and Reed 1952). We have already mentioned the relation of a knowledge of dispersal to the important problems of plant geography. In addition, Wulff (1943: 144-149) has demonstrated the usefulness of a knowledge of life cycles in inferring the place of origin, migration, and relic status of a species. The fact that the distribution of a species is very often or perhaps usually limited by some weak point in the adaptation of a particular stage of the life cycle is generally recognized. This would imply a need for greater emphasis upon the more neglected stages of the life cycle in order to adequately explain plant distributions.

The close relationship existing between taxonomy and autecology has been mentioned by several taxonomists and ecologists (Cockayne and Allen 1927; Turrill 1938; Summerhays and Turrill 1939; Salisbury 1939, 1940; Davidson 1952). It would seem that the work of the biosystematists could be appreciably speeded by greater cooperation with autecologists, who

might eventually provide much of the ecological data basic to modern classification. In this connection it seems that some ecologists have been rather reluctant to accept in practice the recognition of significant ecological diversity resulting from genetic differences to be found within species (see reviews by Baldwin 1942: 35-39; Stebbins 1950: 42-52). The logical conclusion for ecologists seems to be that the local population represents the valid unit for life history studies of species, and consequently that generalizations about an entire species should not be carelessly made on the basis of results from only a single locality. This has been emphasized by ecologists (Lawrence 1950) as well as by taxonomists (Camp 1942, 1943; Fosberg 1950; Davidson 1952). It is to be hoped that wider recognition of this fact will stimulate rather than discourage ecological life history studies, for the need and the challange remain.


## Summary

Some of the more important ecological problems relating to the life history of seed plants are discussed, with citation of key references, for each of the following life cycle stages: seed, seedling, juvenile, reproductive, and senescent.

Problems relating to the life cycle as a whole include that of deciding what process or stage of development is the most critical in the life cycle, and that of the relative roles of internal and environmental factors in determining the course of the life cycle stages.

The seed stage presents problems of dispersal, dormancy, and survival, while the seedling stage involves the ecology of germination and the establishment of the normal nutritional pattern for the species.

Questions of importance for the juvenile stage include that of the causes of mortality and the relation of this to natural selection, and the relative development of root and shoot under natural conditions.

In addition to the usual problems of physiological ecology, the mature or reproductive stage presents special aspects, such as the ecology of vegetative reproduction, of flowers and fruits, and of the quantitative phases of seed production. The senescent stage brings up questions of how ages of plants can be determined, and the causes of death in nature.

Two major types of approach to life history studies are distinguished, and the relations of these to other pure and applied sciences considered.


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## THE OCCURRENCE OF THE CLADOCERAN *LEPTODORA KINDTII* IN COLORADO[1]

Although there are numerous accounts of the water flea, *Leptodora kindtii* (Focke) in the United States (Forbes 1882, 1886; Kingsley 1886; Herrick and Turner 1895), no Colorado records are known. It is the purpose, therefore, of this paper to report the several new occurrences of this organism in this State, and to comment on the peculiarities of its distribution.

All Colorado specimens of *L. kindtii* have been collected in Parvin Lake. This artificial lake, impounded in 1927, is located in the north-central part of the state, at an elevation of approximately 8200 feet. It has an area of 73 surface acres and its maximum depth is about 34 feet. The single basin is somewhat bowl-shaped and there are extensive shoal areas which contribute to the relatively high productivity of the lake (Olive 1953). In general, the physical characteristics of Parvin Lake are similar to those of lakes in Minnesota, Wisconsin, and Michigan in which *L. kindtii* frequently occurs.

In July, 1949, the first specimen of *L. kindtii* was recovered from the stomach contents of a rainbow trout. No other specimens were collected until the summer of 1950, at which time 16 individuals were found in plankton samples (Table I). A total of 20 specimens was found in 1951, whereas in 1952 forty-one

[1] The author wishes to thank the Colorado Department of Game and Fish for making this study possible.

TABLE I. *Numbers of* Leptodora kindtii *collected by month and year.*

| Year | May | June | July | Aug. | Sept. | Oct. |
|---|---|---|---|---|---|---|
| 1949.. | — | — | 1* | — | — | — |
| 1950.. | — | 8 | — | 8 | 2* | — |
| 1951.. | 20 | - | — | — | | — |
| 1952.. | 1 | 10 | 13 | 12 | 4 | 1 |
| Total 80 | | | | | | |

*Recovered from trout stomachs.

of them were taken. The latter number is undoubtedly accounted for by the fact that during the summer of 1952 a 10-liter Juday plankton trap was used for collecting instead of the 1- and 3-liter Kemmerer-Juday water samplers used during the previous years.

There is considerable evidence that this population of *L. kindtii* is an isolated one. For example, no specimens were collected in the several lakes near Parvin, nor has this organism appeared in the plankton of some 80 widely scattered Colorado lakes which have been sampled by the author. Moreover, R. W. Pennak and his students at the University of Colorado have failed to collect this plankter in samples from 100 or more northern Colorado lakes (personal communication). If this extension of range has come about accidently the most likely distributing agent would be tourist-fishermen. Many of these fishermen come from areas in the lake states and middle west in which *Leptodora* is indigenous. Also, many of these anglers use live bait such as minnows and other aquatic organisms. Undoubtedly, this cladoceran has been poured into the lake when some fisherman discarded the contents of his minnow pail. It would appear from the foregoing data that the habitat is suitable and that *L. kindtii* is a well established element of the plankton in Parvin Lake.

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## SOME USES OF VEGETATION MAPS[1]

Good vegetation maps are very expensive. This is so because any really good and useful map, especially if printed in colors, requires much knowledge and skill, much energy and patience in its field work and compilation, drafting, and printing; as a result, very large funds are needed. The production of vegetation maps in the United States has not been significant to date, either in quality or in the number of maps published. One is led to believe that such maps are too expensive compared with their possible use.

It is therefore a startling revelation to find that in Europe many excellent vegetation maps are being published, and now more than ever. Today the United States is unquestionably the wealthiest country on earth; nor is there any doubt that nations like France, Germany and Austria have had their economies seriously crippled by war and destruction, by occupation and huge payments of all kinds. One might argue that these European countries can ill afford what appears to be a luxury, whereas the production of vegetation maps in the United States should meet with few obstacles, if any.

An investigation of this matter reveals that good vegetation maps are far from being a luxury; that, indeed, they appeal to the economy-minded. By bitter experience the Europeans have been forced to economize to a degree that amazes many observant Americans. Under this pressure of harsh circumstances the Europeans have discovered that good vegetation maps will save them millions of dollars. It has been found that these expensive colored

[1]Over the years, many friends and colleagues have contributed to the ideas and examples given in this paper, and it is no longer possible to trace every thought to its source; my gratitude is gladly offered to all contributors. But I do feel urged to express my special thanks to L. Emberger, H. Gams, H. Gaussen, R. Knapp and R. Tüxen, whose stimulating suggestions have been of real benefit to my work.

maps, which, incidentally, have a high esthetic value, cost but a fraction of the expenses incurred without their use.

Vegetation maps satisfy two groups of interests: (1) they are inventories of plant communities existing at a given time and place; they show the areal distribution of vegetation types in the landscape and thereby the extent of what is valuable and desirable, and what is not; and they show the relation of topography to the distribution of vegetation. (2) Through proper use and interpretation of the information on vegetation maps it is possible to plan future action with regard to optimal land use, where optimal implies the best adaptation of land use to the requirements of the people at any given period, and also qualitative and quantitative maxima of production without damage to the soil and water economy of the landscape. "A qualified analyst looks through a vegetation map into the habitat of plants even as a physician looks through an x-ray screen into the human body." (Tüxen.) Vegetation maps permit man to work in harmony with nature rather than against or in ignorance of it.

Vegetation maps are used for a great variety of purposes. It does not follow that there are as many types of vegetation maps at there are purposes to which they are applied; but it does mean that vegetation maps are highly flexible instruments. They can be prepared according to a variety of methods, and as soon as the purpose for drawing the maps has been clearly established, it is then possible to select an approach to the preparation of the map that will assure the greatest satisfaction.

The immediate usefulness of a vegetation map rests on the fact that it shows the distributional aspects of vegetation, and that plants and more especially plant communities indicate the complex features of climate and soil. Instruments, even the most accurate ones, can give no more than a fraction of the information needed. Plants, on the other hand, rooted in the soil and exposed to the daily weather conditions of all seasons report the nature of the environment much more comprehensively. The presence or absence of given species, their appearance, the pattern of their distribution, their association with other species and many other features tell a story which is of fundamental value to all who deal with the land and what grows on it. Indeed, nothing permits one to appreciate the character of the land more readily and completely than the vegetation itself.

To illustrate: it is extremely difficult, even for trained pedologists, to establish the nutrient value of wet soils and, more especially, the areal extent of wet soils of similar nutrient value. An endless number of chemical analyses is inevitable. But the vegetation reveals at a glance the entire environmental complex including the soil type, the physical and chemical characteristics of the soil water, as well as the climatic and biotic features of the habitat.

Vegetation maps are not a panacea for all land use problems. However, as more knowledge is accumulated concerning the preferences, requirements and tolerances of plants and plant communities, it becomes easier to exploit a vegetation map to capacity; and as our knowledge of the indicator value of plant communities grows and deepens, the interpretation of a vegetation map becomes more efficient. It follows that the greater the number of published vegetation maps the more economical is the use of the vegetation maps published later.

Essentially, there are two prerequisites for the preparation and application of vegetation maps: (1) a properly trained staff to handle the field work and all cartographic aspects and (2) qualified persons to interpret the map. Such skills are available in Europe. Unfortunately, there are in the United States at the present time far too few schools for training appropriate personnel, and this lack of skilled technicians is felt keenly. This is an important consideration because vegetation maps are intricate instruments which cannot readily be used by the layman. The rapidly increasing application of vegetation maps in Europe means also that there must be a growing number of people who can prepare, analyze, and interpret them, so that the information on the map can be grasped and exploited to the fullest advantage even by people who are not trained in the study of vegetation. Whenever a vegetation map order is filled, whether for governmental or private organizations, the map is accompanied by a detailed written report, with analysis and interpretation of all relevant features.

Vegetation maps are economic maps because the character of many plant communities is more or less the result of human activity. Also, vegetation maps point to possibilities to improve the use of the land. The maps are used by various branches of the government, by commercial concerns, and for research. So great has been the demand for vegetation maps in Europe that research frequently lags behind; the available man-power is employed almost entirely to fill the steady and ever-growing current of orders. Clearly, it would be wise to make adequate funds available to large-scale and continuous research programs. The deeper the insight into the problems of vegetation mapping, the greater are the returns on the invested capital. It is a false economy indeed that places its resources at the disposal of immediate exploitation without availing itself of the much greater gain which unhampered long-term research assures. But, at last, some people with a variety of interests are beginning to appreciate that the vegetation map is a new

application of science serving the economy and the defense of the nation.

In the following paragraphs a number of examples will be given to indicate the utility of vegetation maps.

### Forestry

One of the basic differences between forestry and any other form of land use is the time involved to produce a crop. Grasslands and cultivated fields permit a harvest after a few months and the much slower orchards and vineyards after a few years. But in the case of forestry it is not unusual to deal with one, two, or even three human generations before a crop has matured to its greatest value.

This places the forester in a difficult position. He must know just how to manage his forests, select his trees, utilize whatever habitats are at his disposal, and plan for a harvest 60-100 years from planting time. A mistake may not be recognized until decades have passed and the resulting losses can be severe. No quick correction is possible, for any change of direction again takes long periods before producing the desired results.

The forester is therefore extremely interested in the physical character of his area and he must know climate and soil in all their details and as comprehensively as possible. As the environment cannot be grasped in all its facets, it is both simpler and more useful to start with the vegetation as it occurs. Plant communities portray faithfully whatever benefits an environment may offer, as well as its limitations. Vegetation maps on the largest scale permit a clear mapping of trees and also of the undergrowth and even the ground cover and are the surest device for understanding the nature of the local environmental conditions. With such vegetation maps at hand one can avoid mistakes, at least the more serious ones, and at the same time manage the forest for sustained maximum yield.

Many of the forester's activities can be based on the interpretation of vegetation maps, notably the selection of tree species, especially if these are not native to his area, and all problems related to afforestation. Furthermore, the density of the forest must be controlled, as also the application of fertilizer and the maintenance or the changes in the chief soil characteristics. Whether these are beneficial or not is soon indicated by the resulting ground cover which warns the forester if he has gone too far in his practices or is going in the wrong direction.

Some tree species may be damaging the soil, especially if the trees are not native to the area or are planted in pure stands. As soon as the ground cover indicates such a danger, a new map should be prepared to establish the extent of the area affected.

The idea of mapping the vegetation of an area periodically, perhaps every 10 or 20 years, is particularly valuable where the forest is not closely related to the climax communities. For the proper recognition of a successive stage in the development of the forest has important bearing on forest management.

This, in turn, leads to the afforestation of waste land where the introduction of species of the local climax has repeatedly led to failure. It seems necessary in many instances to get one of the earlier successional stages established first and, in the protection of this, proceed to plant the species that are ultimately to make up the forest composition.

As a vegetation map permits direct conclusions on the nature of the habitat, it is a useful device in making an appropriate choice of seeds; this has become one of the more critical problems since the recognition of ecotypes.

Some foresters are now promoting "site classification," and in this field the works of Hills (1952) and Westveld (1951) are especially interesting. But the detailed vegetation map remains the most useful and the most practical tool in the hands of all concerned with forest management, as the site qualities are most readily understood by studying the vegetation.

In this country, the United States Forest Service has been the agency most concerned with the improvement of forest management. Its nearest approach to vegetation mapping is the publication of a variety of forest type maps; unfortunately however, these are limited in their applicability. Of late, lumber and paper companies, too, have begun to realize that scientific practices can increase production and permit a sustained yield; their next discovery should be that vegetation maps will pay dividends, too.

### Agriculture

No one is so constantly concerned with the welfare of our crops and pastures as the farmer. He supplies food for the nation and forever endeavors to produce maximum crops. Whatever may be said about market conditions, the work of plant breeders and other factors that affect his production, basically the farmer depends on the relations between his crop plants and their environment. If continuous optimal conditions are to be achieved for these plants, an intimate knowledge of the environmental complex becomes imperative.

Every landscape has its natural vegetation. In very many regions this has now been replaced by semi-natural plant communities or the entirely "artificial" ones of the cultural landscape. However, the cultural landscape is not so artificial as might be suspected and a definite relation exists between the crop plants and the

climax vegetation of an area. Even as the free play of the ecological factors will at last result in a vegetation that is in harmony with its environment and so attain a certain stability, so any given landscape has its particular crops that give better results than all others. Once the indicator value of plant species and communities is known it becomes possible to draw quantitative conclusions, especially with regard to cultural influences grazing, fertilizing, trampling, burning) which are difficult to grasp by purely inorganic analyses. Since vegetation maps can reveal the subtle relations between plants and their environment as nothing else will, a few examples may suffice to illustrate how the knowledge gleaned from these maps can be applied profitably.

A vegetation map of grasslands, pastures, and hay fields presents first of all an inventory of what is available, its value and its distribution. It shows the proportion of grass and forb species and permits close estimates of yield and nutritive value.

In addition, the vegetation map can show much more. It can indicate whether a pasture has been overgrazed and to what degree. It can give an accurate figure for the carrying capacity of pastures in different seasons, and it can show what improvements are possible such as an increased yield. The vegetation map may also indicate what other use of the land now in grass may be made, perhaps more profitably, without doing damage to the soil or in some other manner threaten the future utility of the land.

As in the case of forestry, permanent plantings require special attention. Whenever erosion control is practiced, from seeding gullies and planting them with shrubs to the broad shelter belts that break the force of the wind, it is clear that not just any species will be satisfactory. Where large scale vegetation maps are available, it is much simpler to make an appropriate choice of seeds and trees and prevent undue losses. Many shelter belts were planted in the plains west of the Mississippi after 1933 and of these only a portion fulfilled the hopes that had been based on them. A proper interpretation of the local vegetation would have spelled a far greater success, but no adequate vegetation maps were at hand.

Many people who use the term vegetation think only of forest trees, natural prairies, and the like. This is to ignore the fact that the "cultural" vegetation can be quite as significant as "wild" plants. The cultural vegetation includes the crops and also the ruderal plant communities, *i.e.,* those growing along highways and railroads, on abandoned lots, and similar places. Last but certainly not least, it includes also the segetal plant communities, *i.e.,* the weeds.

All too often the value of weeds is ignored and yet, they are the best indicators of the condition of the cultivated soil. Like all other plants, weeds do not grow just anywhere, and they invariably occur in definite combinations. These weed communities are a keen indicator, showing areas of equal potential yield (whether of crops already planted or to be planted). At the same time a detailed knowledge of weed communities is a powerful aid in weed control.

Two additional examples will serve to further illustrate this point. A large industrial concern produced a commerical crop on an area of modest size. As the prices for this crop rose rapidly during World War II, the concern bought all the surrounding land for a considerable distance and extended the cultivation of the crop. This extension was a complete failure. A vegetation expert was consulted and his investigation revealed that the land was not suitable for cultivation except in a few limited areas. He was ordered to prepare a detailed vegetation map and to make a report. The map showed that only the originally cultivated land and a small number of isolated pieces of the more recently added land were fit for cultivation whereas the rest was suitable for pasture only. As a result the company sold its holdings, after having lost a great deal of money. The speculative character of the company's move could have been avoided had the vegetation map been prepared before, not after, the move was made.

An altogether different use of vegetation maps was introduced in a certain region of southern France where a particular type of hay was especially valuable and therefore commanded a high price. Gradually, hay from other regions and of inferior quality was sold under the name of better hay. The government was asked to regulate the matter and the result was a series of vegetation maps which indicated the floristic composition of the meadows. One could then see at a glance where and only where the superior hay could be produced. The use of the name of the better hay is now restricted to the proper areas.

### Land Management and Planning

Vegetation maps can be very useful tools in managing and planning the utilization of the land. The economic development of an area implies a change in the existing land-use. It means that present methods of exploiting the plant resources of a region must be improved to assure a greater yield, which can be sustained through the years. Therefore the economist needs information on climate and soil, on the natural vegetation, and on present land-use. The economist has come to rely on statistics, but these do not reveal any areal or regional patterns. On the other hand, a vegetation map

does just that and can express statistical material as well.

The intelligent use of the land and optimum results require a detailed knowledge of what and how much the land can produce under given circumstances. It requires furthermore that the land use be managed so as to insure continuity of high yields. Not only is it necessary to conserve existing resources of soil, water and vegetation but also to analyze the condition of each with an eye on amelioration. Groundwater might be abundant and permit irrigation or a greater carrying capacity of the pastures. Forest land may be made to produce a higher income if changed into cultivated fields, but the reverse may be true, too.

Perhaps land should be permitted to become suburban or be changed into industrial sites; but the expansion of housing projects and industries must not unduly encroach on the most productive agricultural land. A good and detailed vegetation map will not only reveal the present conditions of the vegetation but the potential land use at its optimum as well; it will save a planner innumerable time-consuming trips into the field and appreciably reduce his expenses. At the same time, the planner can look froward to results which statistics of soil and climate can never promise.

Public and private agencies concerned with the construction of dams, canals, reservoirs, irrigation, or drainage frequently pay enormous indemnities to land owners on whose land the level of the water table was changed as a result of these activities. When vegetation maps are carefully prepared before and about five years after completion of such projects, they reveal the character and exact extent of the damage. Sometimes the supposed damage does not exist or is limited to small areas. In some cases there may even be an improvment with greater yields than before! And so vegetation maps permit the determination of a fair compensation and may reduce this appreciably (at times to less than 5%!).

There are instances in which the construction of dams, of drainage canals, etc., can do more harm than good, because the damage done to the affected land may be greater than the anticipated benefits of the project. Of course, a vegetation map permits a clear and detailed analysis of the conditions as they prevail before the project is undertaken. But often, experienced analysts can predict conditions that will exist after completion of the project. Thus, serious harm can be avoided; possibly the entire project is abandoned.

Countries which are located in regions with mountains of alpine character are often subject to great calamities caused by floods from suddenly melting snows and glaciers or by avalanches. In the densely populated Alps, the losses are invariably high, and huge sums have already been spent in attempting to prevent the recurrence of such disasters. The extraordinary snow masses which accumulated during the winter of 1950-51 and the record loss of life and property that resulted from the unusual number of avalanches, point out only too forcefully that attempts at prevention had been only a partial success at best. But even before this disastrous winter people had come to realize more and more that the proper management of vegetation is a far more effective agent in subduing snow and streams. Now the Austrian government, through the Bureau for Control of Streams and Avalanches (Wildbach- und Lawinenverbauamt) of its Forest Service, has commissioned proper experts to prepare vegetation maps of the entire country of Tirol on the scale of 1:25,000!

### Pedology and Geology

Both the geologists and the soil scientists have long recognized the necessity of mapping the results of their field explorations. Or else, in some district, the presence of particular mineral formations, such as coal-bearing strata, is suspected but their exact location yet to be determined. In most regions of the world, even in many arid ones, the desired data are often hidden under a cover of vegetation and the occasional outcrops may not be sufficiently numerous for mapping, if, indeed, they are present at all. Again and again, however, the close affinity of vegetation to the substratum has permitted the more observant field workers to outline, even in detail, the respective types of rock or soil. The physiognomic features of the vegetation as they appear on aerial photographs make this especially convenient.

An important aspect of mapping the soils or the geology of an area on the basis of vegetation is the enormous reduction in time, hence in cost, that this affords. To be reasonably sure of good results, a pedologist in the past had to test the soil at regular, closely spaced intervals. Even though the soil proved uniform in its character throughout the entire area, all tests had to be made to ascertain this very uniformity and its boundaries. Tests conducted by Emberger, one of Europe's foremost authorities on vegetation, in conjunction with members of the French Geological survey demonstrated that the vegetation could invariably be used as an indicator of soil types. Hence a good vegetation map can be used to map the soil and only one test per vegetation unit is necessary.

In the case of Emberger's experiments there were no exceptions, although these may nevertheless occur. But they are not beyond recognition. For example, in some areas forest and grass are distributed according to the water-holding capacity of the substratum, with the

grass on the drier sites. It may be, however, that a stream runs through the landscape, and its seepage waters suffice to maintain a galeria forest even though grass completely dominates the landscape only a short distance away. If the stream flows in a ravine, a stereoscopic view of the aerial photographs soon reveals the nature of the vegetational pattern and so prevents a misinterpretation of the substratum. For the preparation of large scale maps, such as soil maps or geological maps, or for prospecting and many other activities to which the pedologist and the geologist must devote much time, a detailed vegetation map is a guide that can save funds and greatly simplify the field work. For "it is evident that there will be a broad change in the soil with every change in the regional vegetation." (Hills 1944: 108).

One of the most useful aspects of all pedological work is the study of soil moisture. Unfortunately, it is extremely difficult to map and yet, it is obvious that one should know where an actual or potential surplus or shortage of soil moisture occurs. The vegetation map provides a happy solution because plant communities react sharply and precisely to soil moisture conditions. An example may illustrate how a lack of vegetation maps can lead to great financial losses.

A certain grass species dominates the vegetation of a part of southern France. This grass indicates a slight salinity of the soil; nevertheless, light cultivation is carried on profitably. It was found that the same grass species dominates the vegetation of parts of Algeria and this was taken to mean that there, too, the land is suitable for light cultivation. As a result, elaborate plans for large scale settlement were prepared and pushed forward to the point of laying out streets, building houses for settlers, and construction of public utilities. The total failure of repeated attempts at settlement cost the government as well as private individuals a fortune. Afterwards, vegetation maps of both areas were prepared, and they revealed that the vegetation of one area was quite different from that of the other and that the dominant grass was one of the few species that occurred in both. It also happened that this species has wide ecological tolerances and was therefore unsuited to serve as an indicator. It was a powerful proof that environmental features including soils, should not be evaluated by the presence or absence of one particular species but always by the character of the entire plant community.

## Education

An increasing number of fields of learning are now employing maps. This does not imply that vegetation maps find a use in all these fields. However, the possibilities of applying them are much wider than has been suspected so far.

For example, a vegetation map can be useful to the historian because it reveals the conditions of the landscape which exercise an influence on the development of its settlements, its productivity, and hence its significance relative to that of other areas. A professor of Russian history happened to come across a vegetation map of the Ukraine. When the details and their significance had been explained to him, he delightedly discovered that here lay the explanation for certain aspects of the land distribution among the Russian nobles by the crown.

Botanists, especially ecologists, deal with plant life and find vegetation maps the best device to correlate the plants with their habitat. To train students, visual aids are now considered indispensable and nothing can clarify the plant-landscape relation as well as a vegetation map.

The vegetation is the most important single feature of the landscape and, ever since the memorable journeys of Alexander von Humboldt, geographers have considered the geographic distribution of vegetation an important aspect of physical geography. To study the vegetation means also to study vegetation units, their physiognomy, their composition, their origin and history, their effects on land use, and their usefulness to man. Indeed, no feature of the landscape reveals so much so readily about the character of a region as does the vegetation. It permits the division of the landscape into ecological sections which are among the most significant units of any areal study. To map the vegetation is therefore an extremely useful activity for geographers, partly because of the results that may reasonably be expected, and partly because of the effective training which it affords to students. In 1949, the Association of American Geographers held a symposium on "what graduate students should study." The three participants were generally recognized leaders of American geography; independently, each one emphasized that plant geography or the study of vegetation was one of the essential aspects of geography, and that graduate students should become acquainted with it. It is obvious, then, that for geographers vegetation maps become basic tools.

Vegetation maps of National Parks and all types of areas where human interference in the landscape has been reduced to a minimum are of special educational interest. The analysis of vegetation maps of such reserves reveals the nature of the landscape, it teaches us how the environment acts on the vegetation and the reaction of the latter. Protected areas may be likened to laboratories in which Nature performs all experiments and demonstrations. Their benefits to forestry, agriculture, and land

management are only now beginning to be realized.

In addition to these illustrations, it must not be overlooked that vegetation maps stimulate and advance many other scientific investigations as well. The fields of geology, climatology, pedology, animal ecology, archeology, and others benefit greatly from the information on vegetation maps

### Commercial Interests

Industrial enterprises and financial institutions have not much appreciated the utility of vegetation maps, at least, not so far. And yet, such commercial interests may well derive considerable benefit from vegetation maps that have been properly adjusted to their particular purposes.

All institutions concerned with the investment of funds must do so with an eye on the profits that can be realized and the losses which may possibly be incurred. The amount which a bank may advance for the purchase of a tract of agricultural or forest land is in direct proportion to the productivity of this land and the use to which it is to be put. It is not possible for bankers to be experts in all fields of economic activity with which they come in contact. A good vegetation map with an appropriate commentary will, however, give the banker a sure guidance and protect him against undue losses.

Similar considerations apply to the insurance companies, especially where crop insurance is involved, but also fire insurance, especially in forests. It is now a well-known fact that some species of forest trees burn much more readily and quickly; that a lush herbaceous ground cover hinders the spread of fire (except when dry); and that the composition of the vegetation and hence its susceptibility of fire varies with the seasons. This seasonal variation is again influenced by the structure and the floristic composition of the vegetation at each season. A good vegetation map with an appropriate commentary will not only protect the insurance company against losses, but it permits also a much more accurate calculation of the minimum premiums.

Insurance of livestock is also a problem directly affected by the nature and condition of the vegetation, *i.e.*, the pastures. Poor overgrazed land results in low grade livestock, more susceptible to diseases and of low productivity, whereas an appropriate vegetation permits the farmer to maintain his animals in a better condition. This is to say, the risk of undue losses is minimized, as is the need for high premiums.

The fertilizer industry ought to appreciate the quality and condition of the land as revealed on vegetation maps. For instance, if the vegetation reveals that a tendency toward a lack of soil moisture exists, then lime may be applied only with extreme caution as it intensifies the effects of a drought. The interests of lumber companies (paper, furniture, etc.) have been mentioned in the section on forestry.

### Military Considerations

Militarists like to consider themselves realists. They must be able to act in emergency conditions and plan for these. They are concerned with the movement of men and material and such movement must proceed as rapidly as possible even though regular communications may be destroyed. Furthermore, such movement may have to be concealed from the air. Cross-country movements and the aspects of camouflage and concealment create a vital interest in many aspects of vegetation, especially its physiognomy and structure. Obviously a forested mountainous terrain presents aspects totally different from those in a vast plain of grasslands. One need only compare the immense distances covered by the campaigns in the Russian steppes or the Libyan deserts during World War II with the bloody and obstinate battles for every yard in the jungles of Guadalcanal or in the Hürtgen Forest on Germany's western boundary. Such obvious examples can be matched by innumerable more subtle ones and it is not surprising that military interests in many countries have promoted the preparation of vegetation maps.

### Nature Lovers

A strong interest in "nature" developed among large groups of the lay public as a corollary to the increasing urbanization of the so-called civilized nations. While most city dwellers are content with week-ends or a vacation "in the country," an increasing number of amateur botanists, ornithologists, conservationists, etc., are showing a serious concern for the fields of their respective interest. It is no longer unusual to find "amateurs" whose knowledge compares well with that of the professional scientist and it is this group of so-called nature lovers that is learning to appreciate the value of a good vegetation map. This is no surprise for in addition to the geographic distribution of vegetation types and their arrangement in the landscape, birds, mammals, insects, and many other animals more or less prefer a particular vegetational environment and can be discovered more readily if a vegetation map is at hand. Hunters, too, find such maps useful. The beautiful autumn colors of certain trees such as the sugar maple can be enjoyed under optimum conditions when a map betrays their location. The same goes with the flowers of trees, shrubs, and herbs and as a vegetation map always shows more than one looks for

(not unlike the dictionary!) one's curiosity is constantly stimulated. The popularity of vegetation maps among nature lovers is therefore nothing astonishing, and can be expected to grow as more and better vegetation maps stimulate their taste.

### Conclusion

In conclusion, it may be stated that it is not feasible here to point out all possible uses to which vegetation maps may be put. These uses include all activities which involve the use of land and the growing of plants. Some of the more obvious ones have been discussed. But one must not overlook such items as the fixation with plant life of sand dunes and of river, stream, and canal banks; the planting of highway and railroad dams (and cuts) and of airports; the vegetation control of the right-of-ways of power lines, and many others. All of these activities demand a minimum of expense, and a permanence of planting. One cannot, therefore, plant just anything that may be available. A careful study of a vegetation map of the area will, however, reveal what plant communities should be established and so assure the greatest satisfaction.

Most examples of the utility of vegetation maps presented in this paper have been taken from the European scene because in this country vegetation maps are not yet applied extensively. Indeed, many of the examples may have seemed startling to the American reader who did not suspect such a wide range of applications. On the other hand, it is the purpose of this paper to point out the great variety of uses to which vegetation maps may be put, so that America may benefit from them as much or more than Europe has so far.

Even in the United States, it has become necessary to be economy-minded. To achieve the most stable, secure, and profitable use of the land, it would be well to consider the European experiences and results with great care. To ignore them can hardly be justified at a time when the economy of the nation is strained as never before. The value of vegetation maps can be demostrated from the broad approaches of state planning down to such fine details as selecting an appropriate site for beehives. Vegetation maps are costly items and require experts to prepare and interpret them. But it is less expensive to pay for vegetation maps than to do without them.

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## NOTES ON THE ABILITY OF THE HORSESHOE CRAB, *LIMULUS POLYPHEMUS*, TO LOCATE SOFT-SHELL CLAMS, *MYA ARENARIA*

One of the important items in the food of the horseshoe crab, *Limulus polyphemus*, in New England is the commercially important soft-shell clam, *Mya arenaria*. Hence, the habits of the horseshoe crab are of interest to shellfish biologists.

The predaceous activities of the horseshoe crab have been reported by Turner *et al.* (1949) and observed by the author during the course of various clam transplanting experiments in Plum Island Sound, near Newburyport, Massachusetts. An outstanding exhibition of clam destruction by horseshoe crabs occurred during the summer of 1949. On May 26 and June 2, 16 bushels of clams, averaging 39 mm. in length, were planted in six plots on a flat composed of moderately soft sandy mud and in five plots on a nearby flat of firm sand, bonded with fine silt and shell fragments. Native clams (*Mya*) were scarce on both flats. The round clam, *Macoma baltica*, and the little gem shell, *Gemma gemma*, which also are eaten by horseshoe crabs, were common but the plots still presented an artificial concentration of food for the horseshoe crabs. The planted clams dug in well judging by counts of holes the day after planting. Within a week, however, the horseshoe crabs were swarming over the plots. On June 7, 31 of them were found in three 10 x 20-foot plots on the sandy flat. On the muddy flat the entire surface of the planted area was so thoroughly excavated that square pools of water marked the plots at low tide. When these plots were dug in November, 92 percent of the clams had disappeared.

The concentration of horseshoe crabs on the plots of clams might have been due solely to random movements if during the course of such wandering they found food and stayed

to eat. However, we believe that horseshoe crabs do not dig entirely at random and that they can locate clams at least two or three feet away. Field evidence that such is the case presented itself on June 21, 1951, in the form of tracks left by one horseshoe crab over a series of small plots of clams.

As part of a race and growth experiment, clams had been planted in small plots or groups of fifty in a grid pattern. Each group of fifty occupied a circle about 18 inches in diameter, and the groups were arranged in three rows of 12 groups each, all three feet apart. Chicken wire with one-inch meshes had been staked down over the entire area to protect the clams. When the horseshoe crab tracks were seen, much of the chicken wire had been buried about a half-inch by a layer of fine silt which showed the tracks perfectly.

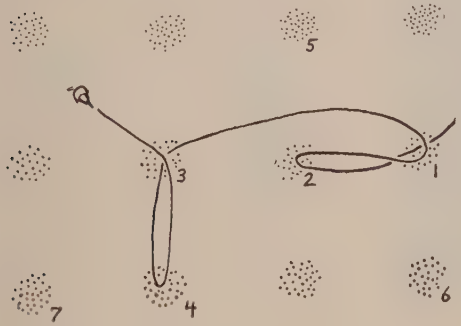


FIG. 1. Diagram of horseshoe crab tracks over 12 plots of soft-shell clams, June 21, 1951. There were crab excavations at all 7 numbered plots, but none at the 29 remaining plots included in the race-growth experiment.

Referring to the diagram (Fig. 1), it may be seen that the tracks started at plot No. 1, then went to 2, then back to 1, then across to 3, down to 4, back up to 3, and then a little beyond 3 where the horseshoe crab was found. If we count the plots visited twice, the crab was "on his target" six times. There was an excavation in the surface mud at each plot visited, exposing the wire underneath and extending below the wire in spots where the horseshoe crab had been trying to dig through the meshes. In addition, there were older water-worn depressions over plots 5, 6 and 7, but no tracks. There were no depressions over the other plots of clams or between the plots, the mud covering the wire in an even sheet except for the small clusters of clam holes extending up through the wire and mud. Therefore, the horseshoe crab did not dig where there were no clams, as might be expected if digging were entirely random. The route of the tracks from plot 1 to 3 is not the shortest route to the nearest clams, but the general pattern of the tracks, plus the fact there were no misses, strongly suggests an ability to locate clams. The two cases where he doubled back to visit plots a second time might indicate a sort of memory.

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## RADIOCARBON DATING OF THE THERMAL MAXIMUM IN SOUTHEASTERN ALASKA

Recent radiocarbon ($C^{14}$) assay of wood buried in muskeg near Juneau, Alaska has enabled a more precise dating of the postglacial thermal maximum in this region of the Territory. Lamont Geological Observatory has given the date as 3,500±250 years (Kulp, *et al.* 1952). The wood was found intercalated in forest peat of Lemon Creek muskeg located on Sunny Point along Gastineau Channel, 7.5 miles north of the capital city. A road, built through the southern part of the muskeg, exposed the peat in section. Since the construction of the road, heaths and other plants have largely covered the exposure. In addition, frost action has caused a certain amount of slumpage to take place. A fresh section about 2.6 meters thick was therefore cut away to reveal the undisturbed peat (Fig. 1). Forest sediments including the dated wood are 0.5 meter in thickness, overlain by two meters of sedge and moss peat and underlain by 0.1 meter of sedge remains. Roots, trunks, and stumps of trees that grew *in situ* constitute the horizon of woody debris. Bottom organics grade downward into gray-green clay with coarser clastics made up of regional metamorphics.

Four peat samples were collected from the exposure: one from the $C^{14}$-dated wood layer

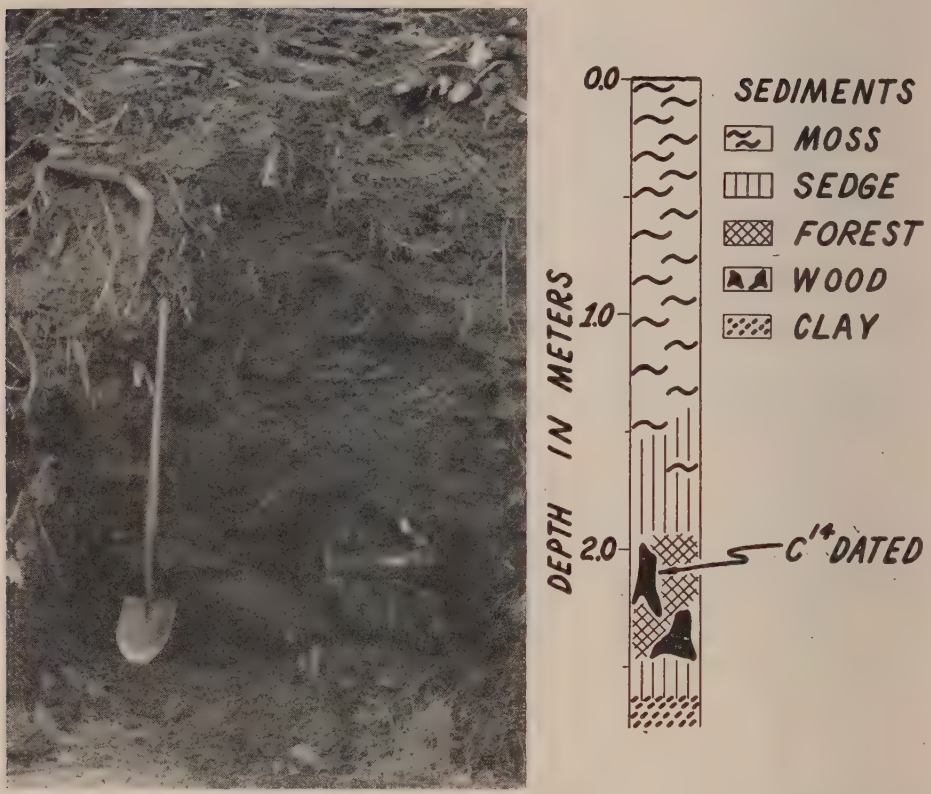
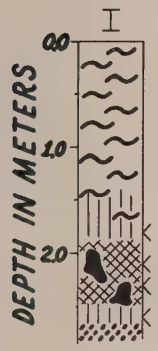



FIG. 1. Exposure and diagrammatic section of sediments at Lemon Creek muskeg near Juneau, Alaska. Radiocarbon-dated wood is shown near the bottom of the section and represents remains of conifers that invaded the muskeg during the thermal maximum.

and one above and two below that horizon. This was done with the purpose of correlating this section with a deeper one obtained in 1950 from the interior of the muskeg. The latter section was excavated through use of a Hiller borer, and pollen profiles and peat heve been described (Heusser 1952). An estimated chronology was projected for the peat of this deeper section, and it is now objective to determine where the 3,500 year old wood stratum rests.

Peat stratigraphy is essentially similar in different parts of the muskeg. This is shown in sections accompanying Figure 2. Section I is 2.6 meters compared with 4.9 meters of section II. The basal portions are comprised of sedge peat. Forest peat is superposed and, in turn, fibrous sedge grades into moss sediments in the overlayer. Stratigraphic correlation of the dated wood is, however, complicated by the fact that the deeper section II shows two forest peat layers separated by sedge. Moreover, another deep section sounded from the east, up-hill side of the muskeg likewise reveals forest strata at two levels with sedge between. In order to correlate the dated wood horizon of section I with the correct forest layer in section II, it was necessary to strengthen the basic peat stratigraphy by means of pollen stratigraphy.

Peat samples were analyzed by first boiling with KOH using gentian violet as a stain. Macroscopic particles were strained out and the deflocculated material centrifuged. Sediments, thus obtained, were mounted in glycerine gelatin and examined on a mechanical stage under the microscope using a lens combination affording 440x. Approximately 150 pollen grains of lodgepole pine (*Pinus contorta*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*Tsuga mertensiana*) were counted from each sample. The percentage of each conifer was calculated based on the total number of grains counted. The grains of skunk cabbage (*Lysichitum americanum*), sedges (Cyperad), alder (*Alnus* spp.), heaths (Ericad-




SECTION I

| 2.6 | 2.3 | 2.1 | 1.8 | DEPTH IN METERS | 4.6 | 4.3 | 3.3 | 3.0 | 2.8 |
|---|---|---|---|---|---|---|---|---|---|
| 4 | 5 | 1 | 1 | Pinus contorta[1] | 2 | 1 | 3 | 2 | 1 |
| 52 | 43 | 40 | 39 | Picea sitchensis[1] | 56 | 49 | 38 | 44 | 41 |
| 36 | 44 | 57 | 54 | Tsuga heterophylla[1] | 36 | 45 | 47 | 46 | 47 |
| 8 | 9 | 3 | 7 | Tsuga mertensiana[1] | 6 | 5 | 12 | 8 | 10 |
| 29 | 24 | 5 | 10 | unknown[2] | 6 | .. | 20 | .. | 10 |
| 91 | 128 | 8 | 22 | Lysichitum[3] | 1675 | 3100 | 3600* | 4 | .. |
| 17 | 4 | .. | 7 | Cyperad[3] | .. | 3 | 6 | .. | 3 |
| 111 | 121 | 6 | 3 | Alnus[3] | 20 | 155 | 600 | 7 | 15 |
| 95 | 45 | 11 | 15 | Ericad-Empetrad[3] | 25 | 60 | 14 | 12 | 16 |
| 1 | 1 | .. | .. | Cornus[3] | 1 | .. | 6 | .. | .. |

SECTION II

[1]Per cent of 150 grain total count for these conifers.

[2]Number of unknown conifers included in 150 grain count.

[3]Number encountered in 150 grain conifer count.

*Approximate number computed by sampling unit slide areas and obtaining an average which was multiplied by total area covered in 150 grain conifer count; applicable to all larger three and four digit figures.

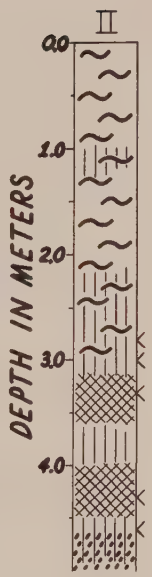



FIG. 2. Pollen stratigraphy of sediments from exposed section I and excavated section II at Lemon Creek muskeg near Juneau, Alaska. Diagrammatic sections are included; sedimentary typology is the same as that in Fig. 1.

Empetrad), and bunchberry (*Cornus canadensis*) were also tabulated in the course of the 150 grain count. Nomenclature follows that of Hultén (1941-1950). Results are presented in Figure 2.

Pollen stratigraphy of Figure 2 discloses that the dated wood at about 2.1 meters in the exposed section I is correlated at approximately 3.0 meters in the deeper section II. This conclusion is reached on the basis of the changes in number of pollens of *Alnus* and *Lysichitum* between 2.3 and 2.1 meters in section I and between 3.3 and 3.0 meters in section II. Alder changes from 121 to 6 grains in section I and from 600 to 7 grains in section II. The most vivid change is that expressed by *Lysichitum* in section II from approximately 8,600 to 4 grains. *Lysichitum* changes from 128 to 8 grains in section I. It should be mentioned that *Lysichitum* occurs in high numbers at all decimeter levels below 3.0 meters to the base of section II. All values between 3.0 and 2.6 meters are low, and no pollen of this arad is found above 2.6 meters. *Lysichitum* seems largely coincident with wood sediments. Numbers of other non-coniferous pollens do not show significant changes. The percentages of the conifers likewise indicate no striking contrasts. All that is shown essentially are the trends of these species in their respective profiles. Although the pollen record reveals that the dated stratum at 2.1 meters in section I was contemporaneous with sedge peat at 3.0 meters in section II (just above the upper forest horizon), correlation of the dated wood is made with the upper forest layer. Apparently *Lysichitum* did not endure in any great numbers during the later sedimentation of forest peat in section I. *Lysichitum* persisted throughout the upper forest horizon of section II.

The position of the $C^{14}$-dated level in section II appears to fit the chronology given for the peat deposit. The interval of the thermal maximum was placed between 4.2 and 2.6 meters on the evidence of wood horizons and charred and oxidized peat. In that it was estimated between 5,000 and 2,000 years ago, the 3,500 year figure is actually the mean of these dates. The upper wood layer between 3.6 and 3.2 meters is likewise a mean between 4.2 and 2.6 meters, the limits of the xerothermic deposit. It is, however, important to state at this point that although this correlation appears sound, the shortcomings resultant from one radiocarbon determination and from the fact that contamination of the sample may occur are to be considered (Bartlett 1951, Flint and Deevey 1951). These results may nevertheless be of value to peat and pollen stratigraphers if they are treated judiciously.

Studies at Lemon Creek muskeg have permitted a reconstruction of the regional history. The site was buried by ice of nearby Lemon Creek Glacier during the last substage of the

Cordilleran ice sheet and in early postglacial time was covered by the transgressed waters of the Pacific Ocean. Just prior to the beginning of the thermal maximum, marine waters regressed and peat deposition began. Rigg (1937) was of the opinion that the genesis of muskeg took place in a saucer-shaped depression, although Dachnowski-Stokes (1941) has indicated its development from a flat. Pollen stratigraphy of the lower and basal peats tends to support the view of Dachnowski-Stokes. No pollen of aquatic plants was observed. This would indicate the absence of early stages of hydrarch succession and of a depression. Instead, an abundance of *Lysichitum* pollen was found at these levels. A poorly drained flat of swampy character is suggested in which *Lysichitum* grew along with sedge initially and later with forest trees.

The sedge deposit that first accrued was invaded in early, middle postglacial time by forest. Wood remains represent the period of the thermal maximum. Climate had warmed and dried to such an extent that forests were able to invade muskeg. Charred wood surfaces reveal the occurrence of fire. Elsewhere in muskegs in this North Pacific coastal district, wood horizons are common indicating a widespread warm and dry maximum. This xerothermic interval lasted an estimated 3,000 years and was brought to a close by the "little ice age". Glaciers of the nearby Juneau Ice Field, such as Lemon Creek, Nugget, Mendenhall, Herbert, and Eagle, were nourished and readvanced at this time. A redevelopment of muskeg is characterized by the late, middle postglacial sedge and moss peats overlying the forest peat. Radio-carbon analysis of interstadial wood buried in outwash of Mendenhall Glacier, a few miles north, has dated the valley segment of the "little ice age" at 1,790±285 years (Kulp, *et al.* 1951). The cooler and wetter climate of this interval has undergone warming and/or drying since the middle of the eighteenth century, as disclosed by the studies of Lawrence (1950). Trees have at present again invaded the muskeg at Lemon Creek.

This paper is a contribution of the Juneau Ice Field Research Project which is directed by the American Geographical Society of New York through contract with the Office of Naval Research. The assistance of the U. S. Forest Service, Lamont Geological Observatory, and Mr. Maynard Miller are gratefully acknowledged. The manuscript was prepared in the Osborn Laboratories at Yale University with the aid of the Theresa Seessel Fellowship.

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## OBSERVATIONS ON THE RATE OF DECAY OF SOFT-SHELL CLAMS (*MYA ARENARIA*)

Some knowledge of the length of time it takes a clam to disintegrate after death is necessary in order properly to analyze field mortality data. For instance, a certain proportion of clams dug may be in various stages of decay, from a relatively firm visceral mass to merely two shells full of evil smelling water. Both of these might be termed "recent," but does "recent" mean a few days, several weeks, or a month or more?

In order to make some approximations of the rates of decay, dead or freshly killed clams were buried in the clam flats of Plum Island Sound, Newburyport, Massachusetts, and dug up at intervals. One batch of clams that had died in the laboratory was buried on January

TABLE I. *The rate of decay of clams in clam flats of Plum Island Sound, Massachusetts—1950*

| Date | Number of Days Buried | Condition of Clams |
|---|---|---|
| WINTER | | |
| *Horseshoe Flat — Hard firm sand, some fine silt.* | | |
| January 16 | 0 | Buried dead clams. |
| April 10 | 84 | Full of soft runny meat. |
| May 5 | 109 | Full of very soft meat, relatively firm at base of siphon. |
| SUMMER | | |
| *Hales Cove — Moderately soft mud.* | | |
| June 13 | 0 | Clams killed and buried. |
| June 21 | 8 | Relatively firm, not runny, very smelly. |
| July 18 | 35 | Traces of rotten meat, some mud, very smelly. |
| *Horseshoe Flat — Hard firm sand, some fine silt.* | | |
| June 19 | 0 | Killed and buried 1-½ and 2-½ inch clams. |
| July 5 | 16 | All rotten, but full of meat. |
| July 10 | 21 | Larger clams full of soft rotten meat. Small clams with traces of decayed meat. |
| August 30 | 72 | Larger clams nearly empty but with mass of cheese-like brown rotted meat. Small clams empty but with mantle periostracum intact, shell not fully clean, no soil between shells. |

16, 1950. Other clams were killed by stabbing them between the shells and twisting the knife, and buried on June 13 and 19, 1950. Periodically, four to six clams were dug from each planting and examined for extent of decay. The results are given in Table I.

The visceral mass disintegrated very slowly during cold weather. In winter and spring, meats were still present within the shells, although partially decayed, after the clams had been buried 109 days. In summer, the meats were even more decayed after only 21 or 35 days.

The size of the clams also affects the period needed for complete decay. Larger clams averaging 2-½ inches in length buried at Horseshoe Flat during June retained meat within the shells for a longer period than did the 1-½-inch clams. Even after 72 days, some cheese-like brown rotted meat remained in the larger shells, while small ones were nearly clean.

The slow rate of decay or disappearance of the meats probably is associated with anaerobic conditions in the flats as well as an absence of scavengers. The oxygen content of the soil was not determined, but general observations indicate that anaerobic conditions prevail. Plant detritus embedded with the silt is usually black or dark brown. Pieces of iron that have rusted away above the soil show very little rust below, and chicken wire fencing which rusts in a summer in sea water will remain strong and bright where buried six inches in the mud.

As might be expected, there was some variability in the rate at which shells fill with soil after the animals decay. In the firm sand of Horseshoe Flat, the shells did not contain soil even after being in the flat 72 days, while in the softer mud of Hales Cove the soil had started to work into shells after 35 days. In other experiments in which live clams were transplanted in April we have found shells completely full of mud two months after they were planted. The date of death is not known in such cases, but obviously the animals decayed and their shells filled with mud in something less than two months.

Table I shows that decaying or nearly disintegrated clams found in the spring may have died during the winter or even the previous fall. Similar clams found in late summer might have been dead one or two months when found. Mortality records should therefore be corrected for the slow rate of decay of buried dead clams.

These observations also suggest the possibility that "mass mortalities" reported at various times may actually have occurred over a period of several months instead of all at one time as often supposed.

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## THE ROLE OF PLANT ECOLOGY IN BIOSYSTEMATICS[1]

As a student of taxonomy I hope I may be permitted, because of the close relationship and mutual interdependence of the two disciplines, to comment on certain opportunities confronting the plant ecologist. Some fundamental concepts and considerations which are now well on their way to incorporation into modern taxonomy seem to me to have profound but largely unrecognized implications for its sister science. From a hurried and highly superficial skimming of ecological textbooks and current periodicals, it has struck me that there are some unhappy parallels between the reactions of taxonomists and ecologists to the impact of data from other biological fields, particularly cytology and genetics.

The reaction of many taxonomists of the past half-century was that, if they kept their fingers in their ears and their eyes focussed strictly on their traditional methods, these interruptions from without would go away. It was contended with some heat that taxonomy was an autonomous subject in its own right, with its own objectives, methodology, vocabulary, and trained practitioners, and that it did not need or welcome either data or advice from would-be interlopers. At worst, this attitude led to a preoccupation with the mechanics of the trade, a highly sensitive inferiority-complex, a general disrespect for the field on the part of other biologists, and the flight of some of the more original minds to greener pastures. Although the "orthodox taxonomist" remains the official strawman and whipping boy for some geneticists and evolutionists—particularly those who are unaware of what has been going on inside taxonomy—he has in reality pretty well disappeared from the scene. In his stead stands a new generation of taxonomists who have largely taken the sting from the attacks of his old tormentors by joining them in the profitable and somewhat more cautious and critical application of novel methods and approaches to the problems of phylogeny and classification.

Like taxonomy, plant ecology is an integrative discipline, which attempts to orient biological and physical data about some common center. In the case of ecology, the unifying principle is the interrelationship of organisms and their environment. For its basic data, ecology—again like taxonomy—is almost wholly dependent upon other disciplines, and the attempt by some to maintain that ecology is quasi-independent of these disciplines and a sub-science in its own right because it has its own objectives, methodology, terminology, and practitioners has the aspect of a losing cause. The erection of even more formidable barriers in the form of elaborate, static classifications and abstruse terminologies is not likely to shut out for long the seepage of biological facts.

It has been stated by some critics that the curse of American plant ecology is "environmentalism," and to the casual observer it does appear that the plants receive considerably less attention than do the physical attributes of their habitat. To quote Egler's recent provocative criticism, "It has been proclaimed by several investigators that if we could understand thoroughly and completely the nature of the environment, then we would understand all the phenomena of vegetation. ... It might be well if a group of fanatics would 'reveal a new truth': that vegetation is the sole result of the inherited characteristics of the plants, and that if we understood everything about the inheritance, then we would understand vegetation. The pendulum might move from its present extreme position."

Many ecological writers in this country appear to limit their curiosity about the vegetable denizens of the all-important environment to lists of species encountered in transects or counted in quadrats and their patterns of horizontal and vertical (including subterranean) distribution. There is little intrinsic evidence in the sources examined that these species are ever visualized in any different sense than they might have been regarded by taxonomists and other biologists of a hundred years ago. Davidson (1952) has recently emphasized that, "A moment's reflection will show that such a view is based upon a concept of species in which all members are genetically uniform; that all members of the same species have the same wide range of tolerance for each of the physiological factors, and the same wide range of morphological expression."

Of the ecological textbooks now popular in the United States, only the Fuller and Conard translation of Braun-Blanquet and the new text of Daubenmire (1947) appear to question this view of species or, indeed, to give any attention at all to their genetic constitution. In his tenth and final chapter, the latter author provides a concise account of the work of Turesson, with an even briefer reference to that of Clausen, Keck, and Hiesey. He says of the former: "These studies by Turesson were an important foctor in bringing about the major revolution in plant taxonomy which is only now well under way, and which for the first time gives the ecologic viewpoint the consideration it deserves in that subscience." More significantly for our present purpose, however, he adds this sentence: "The value of a species as an indicator of particular environmental conditions is highly dependent upon its degree of ecotypic specialization, for the ecotype, rather than the species, is the fundamental ecologic unit." There is very little in the previous nine chapters of his book, however, to

indicate the possibly explosive impact of this second postulate upon ecological objectives, methods, classifications, and interpretations.

I should like to expand a little Dr. Daubenmire's reference to the work of Turesson and of other investigators along similar lines, and to emphasize that ecology is, or should be, affected no less than taxonomy by some of its implications.

### Genecology, Experimental Taxonomy and Biosystematy

Beginning on a modest scale in 1916, the Swedish plant ecologist Turesson (1922a, 1922b, 1923, 1925, 1929, 1930a, 1930b) employed extensive observations of wild plants transplanted into a uniform garden in an endeavor to study the effect of ecological factors in the differentiation of plant species. You will recall that his data led him to conclude that wide-ranging and heterogeneous species-populations are commonly broken up into different clusters of hereditary variants corresponding with the various habitats occupied. This phenomenon he interpreted as being due to the sorting-out and controlling effect of environmental factors which split up the genetically and morphologically diverse species-population into appropriate habitat-varieties. He noted (1923) that ecological advance had hitherto proceeded along two principal lines of attack: that dealing with the relation of the individual plant to its environment, or autecology; and that dealing with the relation of plant communities or vegetation to their environment, usually termed synecology. Turesson emphasized that autecology had been "pursued as if hereditary diversity within the particular species dealt with did not exist." For the study of genetic variation within species and the relation of this variation to habitat conditions, he coined the term Genecology. "From the point of view of genecology," in his words, "the Linnean (that is, the taxonomic) species represents a genetically complex *community*, the distribution and the composition of which is largely determined by the ecological factors and the genotypical constitution of the individuals composing the species-*community*." (Italics supplied by the writer.)

With this background, I was moved to wonder what had ever become of Genecology? So far as I have been able to discover, Turesson's papers were not reviewed in any American ecological journals, and I could not find "Genecology" listed in the index of any of the standard ecological texts—save only for the summary furnished by Daubenmire. One interesting by-product of my otherwise fruitless search was the discovery, however, that the papers of Clausen, Keck, and Hiesey on "Experimental Studies on the Nature of Species" (1940, 1945, 1948) are filed under Plant Ecology according to the cataloging system of the Library of Congress. Needless to say, the librarian responsible for this lacked any formal training in plant ecology.

I think that the mystery of the disappearance of Genecology turns out to be largely a problem of synonymy, something which is reputed to be dear to the heart of every true taxonomist. The first use I have found of the term "Experimental Taxonomy" is in association with the work of Clements and Hall as reported in the Yearbook of the Carnegie Institution of Washington for 1919. Here the statement is made that, "The transplanting of related species, variable species, and ecads to determine the effect of changed and measured habitats in causing adaptation and variation and in producing new forms has been carried on actively." In the previous yearbook, the report by the same authors on the same kind of studies was listed under the heading of "Field and Garden Study of Genera and Species." Clausen, Keck, and Hiesey used the term Experimental Taxonomy for the annual reports beginning in 1934 of their investigations which continued and expanded those of Hall. They do not define the term, but the studies described deal with transplants and complementary cytological and breeding investigations. Furthermore, a special Conference on Experimental Taxonomy was held in the summer of 1934 in which, it is said, "Emphasis was laid upon the species and race problems, evolution, adaptation, endemism, the phylogenetic importance of rare and disappearing species and enivronmental modification." Gregor, Davy, and Lang, two years later (1936) in England, used the term Experimental Taxonomy to cover "the classification of evolutionary units on the basis of experimental facts." Here again, the mode of approach is a combination of transplantation and breeding studies.

Hall and Clements' "The Phylogenetic Method in Plant Taxonomy," which appeared in 1923, stressed the importance of obtaining "a knowledge of the variation of the species concerned throughout its climatic area and of its adaptation as it enters diverse habitats adjacent to the normal one." Also recommended were statistical studies of the species throughout the whole range of natural conditions, and experimental analysis under controlled natural conditions, and in the garden and greenhouse. The phase of study here discussed was termed "Evolutionary Taxonomy," and there is more than a suggestion that the environment was visualized as the primary initiator of genetic variation rather than merely a selecting force.

In their stimulating essay on "The Structure and Origin of Species," Camp and Gilly (1943) duly noted "that already there is with us a

[1] Vice Presidential address of AAAS Section G, St. Louis, December 29, 1952.

new branch of the science of systematics-biosystematy..." The new discipline is described as "the ultimate stage of biological systematics ... wherein the group under consideration, in addition to morphological and biogeographical studies, is subjected to genetic analyses. Here we define the term 'genetic analyses' in a broad manner and include under it such things as cytology in its various phases, breeding tests and (in botany) transplant studies." A few pages farther on we are informed that, "Our concepts have been based upon two primary criteria: (1) the appearance of species-populations in the field and (2) the genetic systems operative within these populations."

I think we may now feel quietly confident that we have run to earth Genecology, or something very like it, despite the aliases and somewhat various disguises that have served to keep it well hidden, at least from many plant ecologists. It is beside the point to argue as to whether such terms as Experimental Taxonomy, Experimental Evolution, and Biosystematy are necessary or accurate. The important concern is that Genecology slipped away from the realm of plant ecology to that of plant taxonomy, to the great gain of the latter and the great, if still largely unrecognized, loss of the former. Under whatever name we group these similar approaches, it is clear that they imply findings of undeniable significance for ecology.

There are two aspects of these, one of which may be regarded as largely negative and precautionary at the present time, the other as distinctly positive and invitational. The fact that species and other taxa are now almost universally regarded to be assemblages of morphologically, genetically, and physiologically diverse individuals destroys the satisfying but erroneous view of what Egler ironically refers to as "our simple species that left the Ark." The impact of this newer conception upon the indicator value of species is obvious, and its effect upon the elaborate systems of synecological classification is something to be pondered. Clausen, Keck, and Hiesey state (1941) that, "From the point of fitness to the environment it is evident that the ecologically important unit is not the species, but the regional climatic race, or ... ecotype," an opinion which Daubenmire has echoed. Whether or not this view attaches too much importance to the climatic ecotype, it is certainly abundantly clear that the morphological aspect of a plant is no safe guide to either its physiological or genetic behavior. As Salisbury has remarked (1940), "To the ecologist ... the physiological characters, some of which may have no visible manifestations, are fundamentally the most important, whilst the visible features of external morphology and internal structure are for him mainly significant in so far as they represent, or are concomitants of, the physiological or biological equipment of the species concerned that affects its relations to the habitat conditions, either physical or biotic."

Quite apart from the precautions for current ecological practices that emanate from Genecology, there is a decidedly positive aspect. Why should not plant ecologists as well as geneticists, physiologists, cytologists, or taxonomists be the ones to exploit this field of endeavor which has yielded so many valuable data for a better understanding of cytological and genetical phenomena, and hence for evolution and taxonomy? The field was first conceived as a combination of ecological and taxonomic investigation, and was first staked off and productively tilled by ecologists. Park, in his "Observations Concerning the Future of Ecology" (1945), calls for full collaboration by the ecologists with geneticists and taxonomists on the problems of evolution. This is the first of the great opportunities I see facing plant ecology.

## The Problem of Suitable Ecological Classifications

So long as autecology deals with the individual organism alone, the general taxonomic system may suffice for its purposes. The synecological classifications have been seen, if we may borrow a phrase from the recent political campaign, to be standing on a barrel of eels. There is little likelihood of achieving a firmer foundation for them until there has been a more widespread recognition of the complexities of natural populations and the development of special classifications adequate to the purposes of ecological investigation. It has been abundantly shown during recent years that no series of definitions can make the many different kinds of natural populations coincide in morphology, cytology, breeding behavior, and physiological characters. As Turrill has emphasized (1946), "... taxonomy has to have a wider basis than genecology, ... (and) while genecological research has much to contribute to taxonomy, genecological classification, if strictly adhered to, is a special and not a general classification...." Inasmuch as the ecologist's "requirements may demand a segregation of types distinguished far more by their physiological characteristics than by their morphological features" (Salisbury 1940), the absolute reliance of ecologists upon morphological taxa is no longer defensible.

Because the species concept of the taxonomist frequently conformed only poorly with the situations observed in his cultures and in nature, Turesson promulgated his well known coenospecies-ecospecies-ecotype classification. Turrill (1946) and Valentine (1949) have recently

called attention to the extent to which this classification based on primarily ecological definitions has undergone progressive modification, until the ecological aspect has become almost wholly subordinated to the genetical. In 1922, the ecospecies was a term designed "to cover the Linnean species or genotype compounds as they are realized in nature," the coenospecies was "the total sum of possible combinations in a genotype compound"—that is, a hypothetical entity *not* to be found under natural conditions—and the ecotype was a name "to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat." By 1925, this investigator had observed strikingly parallel hereditary habitat types shown by totally unrelated species but which occurred together within the same kind of extreme habitat. He proposed a series of artificial categories for the more striking of these, for example, *oecotypus campestris, oecotypus arenarius, oecotypus salinus, oecotypus alpinus,* etc., as "an endeavour to found a natural system of life-forms." By 1929 the ecospecies had become, "An amphimict-population the constituents of which in nature produce vital and fertile descendents with each other, giving rise to less vital or more or less sterile descendents in nature, however, when crossed with constituents of any other population." A coenospecies had been transmuted into, "A population-complex the constituents of which group themselves in nature in species-units of lower magnitude on account of viability and sterility limits having all, however, a common origin so far as morphological, cytological or experimental facts indicate such an origin," and *Capsella bursa-pastoris* and *Erophila verna* were cited as illustrations of coenospecies. The ecotypes, by 1930, have become "subspecific units originating through nature's own grouping of the biotypes." By this time, also, Turesson has dismissed phylogeny as an unworkable criterion for systematic classification in favor of his genecological units "based on genetical and ecological inquiry," adding that "natural definiteness of biotype-groups does not necessarily involve common descent."

Clausen, Keck, and Hiesey in 1939 defined cenospecies on the presence of absolute internal genetic barriers, ecospecies on a combination of genetic and geographic or ecologic isolation, and ecotypes on purely geographic or ecologic isolation. In this and their other papers, Clausen, Keck, and Hiesey have attempted to correlate ecospecies with taxonomic species, ecotypes (if morphologically distinguishable) with subspecies, and cenospecies with the genus or section. Valentine (1949, 1950, 1952) finds the ecospecific category too broad, ranging "from almost complete hybrid fertility at one extreme to almost complete sterility at the other," and suggests the need for a subdivision of this category into "*g*-ecospecies" and "*a*-ecospecies." The former are believed to have arisen gradually, without change in chromosome number, from ecotypes; the latter are formed abruptly, by allopolyploidy or a major chromosomal change, and may or may not be polyploid, but are at once genetically disjunct from their parents. Gregor and his associates (Gregor 1938, 1939, 1946; Gregor, Davy, and Lang 1936; Gregor and Lang 1950), working with sea-plantains, have emphasized the occurrence of character-gradients or clines and find that "ecotypic differentiation is more often continuous than discontinuous." For Gregor (1946), an ecotype becomes merely "a particular range on an ecocline," rather than a distinct, climatically determined population.

Whether or not clearly defined ecotypes are a general phenomenon in most species of plants is apparently a debatable problem, and one on which the plant ecologist should be able to throw a great deal of light. Turesson's earlier ecotypes were determined by orographic and edaphic factors, his later ones by climatic factors, but I cannot discover that he ever discussed the relationship between the two. In 1939, Clausen, Keck, and Hiesey were sure that variation was distinctly random, *i.e.,* not forming natural groupings of any kind, within the limits of each climatically determined ecotype. On the other hand, the work of Kruckeberg (1950) among others has shown that a single climatic ecotype may contain more than one edaphic ecotype, and there are now well recognized biotic ecotypes which appear to be maintained by grazing and other agricultural practices. In their work on *Achillea* (1948), Clausen, Keck, and Hiesey seem to be less sure than formerly of the indivisibility of climatic ecotypes. The yarrows were found to have at least eleven diverse and variable climatic races along a 200-mile transect in California, and it is suggested that the number of these in the total range of the three species recognized "may easily run into hundreds." Snyder (1950), working with *Elymus glaucus* in the Sierra Nevada of California, found that on the basis of intersterility the twenty strains studied would necessitate the recognition of fifteen ecospecies, one with four ecotypes, one with two, and the other thirteen ecospecies with one ecotype each.

Clearly, the occurrence of ecotypes within ecotypes, the existence of climatic, seasonal, edaphic, and biotic ecotypes, and the new evidence as to their probable number in some wild species, raises a serious question as to whether or not they afford any reliable basis whatever for taxonomic classification. It has even been suggested that an ecotype may be an artifact produced by the method of sampling, or that

ecotypes are features only of those areas (like California) where a great range of habital extremes may occur within short distances. Turrill (1946) suggested that the ecotypes of Turesson and those of Clausen, Keck, and Hiesey were of a completely different order of magnitude and not at all comparable. In his latest and excellent publication (1951), Clausen puts the emphasis on "physiologically distinct races" and recognizes that these may or may not be morphologically distinguishable.

Without belaboring the matter further, it is clear that the construction of adequate ecological classifications of species-populations as they occur in nature is by no means a finished task. Although it has been left in recent years largely to the geneticist, the cytologist, and the physiologist, it needs the help of the ecologist, who must be vitally concerned with the results. This is a second opportunity I see facing plant ecology.

### Natural Hybridization and Introgression

The occurrence of plant hybrids has interested botanists for nearly two hundred years, but the question of their frequency and importance under natural conditions is by no means settled. Most taxonomists and ecologists of previous decades have been inclined to feel that hybrids played too minor a role to cause any real concern. However, the subject has refused to stay prematurely interred, and has returned to haunt the student of floristics.

A great stimulus has been given to the study of hybridization in the last few years by Anderson's invention (Anderson and Hubricht 1938) and espousal (Anderson 1949) of "introgression," that is, the flow of genetical materials across a barrier from one population into another as a consequence of successful interbreeding. This author has laid particular stress (1948) on the significance of human activities in preparing ecological niches for the reception and preservation of products of dubious parentage. With his unfailing flair for the dramatic, Anderson has titled this the "hybridization of the habitat," twisting the tail, so to speak, of one of ecology's sacred cows. Man's activities in upsetting natural equilibria appear to have set the stage for a mongrelization of the native flora, although it seems likely that such nonhuman catastrophes as glaciation, flood, fire, and the like may have long had a similar effect. There are now abundant data at hand to suggest that many of our forest trees, such as pines, maples, beeches, ashes, and oaks; our shrubs, huckleberries, service-berries, sages, and blackberries; and our herbs, irises, primroses, tradescantias, pinks, asters, fleabanes, and goldenrods, owe their present constitution to the consequences of such hybridization (Anderson 1949, Heiser 1949b). It is now well established that allopolyploid species have arisen suddenly in nature as a result of natural hybridization, and some (Lewis and Epling 1946, Constance 1950, Epling and Lewis 1946) have even had the temerity to suggest that some diploid species, also, may have arisen in a similar manner.

Anderson tends to regard introgression as perhaps more important than the origin of new mutations in maintaining the variability and hence the adaptibility of natural populations to environmental conditions. He suggests that a sort of scarcely detectable genetic trickle, like the flow from a leaky faucet, between one population and another may have more profound consequences than the type of spectacular hybrid swarm that catches the eye of any field observer. If the genes thus transported happen to be those controlling the physiological attributes of the plants involved, their importance in ecology will be apparent. Another interesting aspect of this problem is the involvement of weeds and cultivated plants in the complicated genetic interchange.

It might once have been a valid position to maintain that such phenomena were only the results of disturbed environmental conditions, and hence of little concern to those working with natural vegetation. However, it now appears questionable how much "natural vegetation" is left anywhere in the world. Our childhood faith in the quasi-universality and comforting stability of the so-called climax communities has been rudely shaken if not irretrievably shattered. We may be sure that disturbed habitats will continue to become increasingly more, rather than less frequent. Neither the ecologist nor the taxonomist can now afford to devote himself wholly to what he might wish to regard as unchanged conditions. This course would suggest that all ornithologists should specialize on the greater auk, the passenger-pigeon, and the dodo.

The work of Mason (1942) and Zobel (1951) on pines, of Marsden-Jones and Turrill (1946) and Baker (1948, 1951) on pinks, of Valentine (1947, 1948, 1952) on primroses, of Heiser (1947, 1949a, 1951) on sunflowers, and of Woodson (1947) on milkweeds, suggests how an analysis of natural hybridization and introgression may make possible the tracing of floristic and ecological history within certain areas. Introgression, I am glad to say, has already profitably attracted the attention of such investigators as Dansereau (1941) and Fassett (1941), who I believe consider themselves to be at least part-time plant ecologists. It is less clear to me whether the majority of ecologists consider such pioneer investigations to be a legitimate aspect of ecology. Nevertheless, I suggest the field of natural hybridization, in the broadest sense, as a third opportunity confronting plant ecology.

### Ecological Barriers to Interbreeding

Of equal interest from an evolutionary point of view to the occurrence of hybridization in nature is the problem of its failure to occur between plants which can produce fertile progeny under artificial conditions. From their behavior under cultivation it might be supposed that such genera as *Quercus, Ceanothus, Rhododendron,* and *Aquilegia*—to name only a few—would find it impossible to maintain morphologically distinct populations in nature. Nevertheless, they appear to do so quite successfully.

The geneticist has thus been led to an investigation of isolating mechanisms. There have been many classifications of these (Stebbins 1950, Riley 1952), frequently with major groupings under the heads of internal, intrinsic, or genetic as opposed to external, extrinsic, or ecological and geographic factors. The latter grouping involves such items as spatial and habital separation, temporal or cyclic isolation, and the lack of suitable niches in which hybrids may survive. Many instances of the maintenance of morphologically different but interfertile populations appear to owe to a delicate combination of internal and external isolating mechanisms (Baker 1951). As Riley points out, "Undoubtedly many different ecological factors operate as ecological isolating mechanisms and many different combinations of ecological and other barriers must separate species or incipient species in many genera. There should, therefore, be an abundance of material to engage the attention of ecologists, taxonomists, and phytogeographers for many years to come. While the fundamental problems are far better understood and appreciated now than they were a half-century ago, there are still many details to be investigated regarding the specific factors involved and their operation in many widely separated groups of plants."

Grant has recently suggested (1949, 1950, 1952) that in certain flowering plants, for example the columbines, it may be the flower-specificity of pollinating insects which keeps interfertile species distinct in nature. He poses the interesting hypothesis that groups highly specialized in floral structure may, as a general rule, lack strong internal barriers to interbreeding because the bird or insect visitors have provided effective isolation between species by their selective pollination. This theory, as its author is the first to point out, needs testing in many other groups of plants. It may serve, however, as an example of the kind of ecological explanation which might be sought for such problems. The whole problem of ecological isolating mechanisms is surely as germane to the field of interest of the ecologist as it is to that of the taxonomist or the geneticist. The modern ecologist prides himself on thinking in terms of the biome, or the complex symbioses between plants and animals occupying the same habitat. Thus, this fourth and last challenge which I am blithely tossing to the plant ecologist would appear to be peculiarly appropriate to his interests.

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I have heard it argued that plant ecologists are too busy studying plant ecology to have time to train themselves in taxonomy. And, besides, they can always get some taxonomist to identify their plants for them. It may be claimed, also, that the successful prosecution of the kinds of approaches I have suggested here are impracticable for the ecologist, inasmuch as they would require him to become something of a taxonomist, cytologist, geneticist, and physiologist. These are undoubtedly *explanations,* but I should scarcely dignify them as valid excuses! The taxonomist has been called upon in recent years to exercise approximately these same mental muscles, and I have heard nothing to indicate that the activity has done him any permanent injury. Some even seem to feel that it may have done him some good.

An eminent ecologist, Park, has remarked (1945) that "ecologists have 'missed the boat' so many times that the process is becoming habitual." I have attempted to mention here only four vessels, and there are many more, equally seaworthy, which I believe plant ecologists can ill afford to miss, and I sincerely hope that, for the good of all biological science, they will not miss them.

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LINCOLN CONSTANCE

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## ARCHBOLD BIOLOGICAL STATION

This south Florida field station should be better known to American biologists and more fully utilized by them. It offers opportunities for field work with laboratory aids immediately available. It is located in the Florida scrub, about a dozen miles south of Lake Placid and is open all the year around.

The region is semitropical. The native fauna and flora are still to a large extent undisturbed by human hands. The place is quiet, comfortable and sanitary. I have spent seven winters there; several of them, collecting and rearing dragonflies for a new Manual of the Odonata of North America, that is now being published by the University of California Press. Other winters I have spent in the study of small communities: one, the community that lives in the flower-heads of a weed that blooms every day in the year, *Bidens pilosa* (see *Ecological Monographs*, **18**: 431-446); the other, a study (now completed) of the insects associated with, and more or less dependent upon another common weed, *Boehmeria cylindrica*.

In these studies I have been seeking ecological phenomena—not new species; but in their course I have discovered ten new species, mostly minute parasites, but a few larger forms: one a Lygaeid bug, one a Lampyrid beetle; also I have reared a miniature moth of *Machlotica*, a genus not hitherto known from North America. And I seem to have come upon a new example of polyembryony in *Tetrastichus*. All of which indicates that much pioneer work remains to be done in this region.

There is no teaching here. Workers come by prearrangement with the proprietor, Mr. Richard Archbold, and with the approval of his advisory board. They may come for shorter or longer periods, according to the needs of the research they have in hand. Considerable aid may be expected toward finding the habitat of the things desired, but for freedom to roam at will the worker may best come in his own car. A well-equipped machine shop and a carpenter shop are available for construction or repair of apparatus needed for the work in hand. The nominal fee ($50.00 per month) covers all expenses, including board and sleeping quarters.

A descriptive circular is available upon request.

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## Invertebrate Zoology with Paleontological Emphasis[1]

This book should be on the desks of all zoologists and paleontologists, whether they be systematists, ecologists, or what not. Although it is said to be a revised and enlarged, or second edition of Twenhofel and Shrock's *Invertebrate Paleontology,* first published in 1935, it is actually a new book, largely due to the efforts of Dr. Shrock. Whereas the first edition might best be described as fair to middling, this new edition is clearly excellent, and in many ways is not only the best modern text of invertebrate paleontology but also the best text of invertebrate zoology. These last two statements invite discussion.

With respect to the first statement, that this is the best text of invertebrate paleontology, it would perhaps be better to say the better text, for the only comparable book covering the same ground is *Invertebrate Fossils* by Moore, Lalicker, and Fischer, also recently published by McGraw-Hill. The physical differences between the two are small indeed, in price, in size, coverage, volume of words and illustrations, and accuracy of presentation, but more subjectively the Shrock and Twenhofel has the edge in my mind. The pages are printed in single columns instead of the aesthetically irritating double columns of often pompous prose of Moore, Lalicker, and Fischer; the paper is more opaque; the illustrative figures are a balanced mixture of fairly well reproduced half-tones and well-finished line drawings of specified sources, new and old, rather than a monotony of line drawings, usually of unspecified sources, many of which have an unfinished appearance and are reproduced on too large, indeed a wasteful scale. Physically Shrock and Twenhofel is a superior book—although both volumes are alike in having an annoying and unnecessary mode of figure notation. Scientifically the two are about the same, Moore, Lalicker, and Fischer having perhaps a slight edge in coverage of the most recent advances in some aspects of systematics, as for instance the relationships of the carpoid echinoderms, but perhaps the Shrock and Twenhofel is just more conservative. Shrock and Twenhofel is stronger on tables and charts of ranges and relationships of subdivisions of the phyla which give a coherence lacking to some extent in the Moore, Lalicker, and Fischer. Compare, for instance, the chapters on coelenterates in this regard.

With regard to my second point, that this book is the best text of invertebrate zoology, let us see how it compares with the "best" recent text of invertebrate zoology of the same size, coverage, and suitability as a text for a two term course in invertebrate zoology on the same level as that for which the Shrock and Twenhofel is designed in paleontology. This book, hereinafter referred to as the "neontologic text," has about the same number of pages of slightly smaller format and roughly 300,000 words to about 400,000 in Shrock and Twenhofel, and with a shocking disparity in figures in favor of the latter. It is no excuse to say that the student will receive adequate illustrative coverage beyond the text in lectures, laboratory, and in the field. Text illustrations are seen oftenest and retained longest; they had better be good. On the basis of illustrations Shrock and Twenhofel is infinitely superior, even if all strictly paleontologic figures were omitted. I haven't counted them all, but for the echinoderms, to which the neontologic text devotes 37 pages and a total of 62 figures, the paleontologic text gives 94 pages and about 450 figures. Some idea of the adequacy of coverage of this group, extremely important from every point of view, is given by the fact that Shrock and Twenhofel discuss *all* of the twelve classes now generally accepted. Of the eight extinct classes, the neontologic text mentions only five, with no real analysis of their interrelations, with only *one* figure of an extinct form. This in spite of the obvious fact that an invertebrate is an invertebrate, extinct or living, and that one cannot pretend to understand living animals without knowledge of their fossil relatives any more than a paleontologist can know fossils without knowing their remnantal living descendents. This obvious but obscure axiom admits of no exceptions. But to return to the neontologic text's treatment of echinoderms: there is no explanation of the basis of classification of the group, there are no tables of chief characteristics, there is nothing on ecology—one must dig hard to discover that the phylum as a whole is exclusively marine, and there are only a few words on the evolution of the classes or other subdivisions. Don't bother to look for such things as homomorphy or neoteny. Shrock and Twenhofel gives space to all these, including a page and a half on general ecology, and four to problems of evolution. On the whole, I

[1] **Shrock, R. R., and W. H. Twenhofel.** 1953. Principles of invertebrate paleontology. xx + 818 pp., 25 tables, 469 numbered figs., including nearly 3000 actual figs. New York: McGraw-Hill. $12.00.

can't find any essential points covered in the neontologic text not covered by the paleontologic text, although there is some disparity. Shrock and Twenhofel devotes much less space to those tiresome groups, the protozoans and insects, but at least all main groups are described and illustrated. Even the rather exotic phoronids, not positively known as fossils, are given a chapter by Shrock and Twenhofel: 4½ pages and 14 figures, contrasted with a grudging third of a page and five poor figures in the neontologic text. The latter fails utterly *even to mention* such widespread extinct *classes* as the Conulariida, Stromatoporoidea, Tabulata, Rugosa, Trepostomata, Cryptostomata, and Pleospongia, some of which endured hundreds of millions of years and are of just as much significance biologically as the Coleoptera.

To this reviewer (a highly prejudiced paleontologist) it is inexcusable that such a book as the neontologic text touched on above, with its stroboscopic look at the present with the merest glance over the shoulder at the past, should continue to be used when such a book as Shrock and Twenhofel is now available, a book which treats the invertebrates through the hemichordates as if there were no difference between a living and a fossil organism.

A last word. What is there in this book for the ecologists, who must shove over more and more to make room for the paleoecologists? There is little except for those who understand that ecology refers to other organisms than plants, vertebrates, and insects. The authors have devoted a surprising amount of space to the ecology and paleoecology of the marine groups which provide the vast bulk of fossils. Indeed, there is more here on each of the groups mentioned than can be found in any of the common texts of ecology now available. More pages are devoted to the ecology and paleoecology of recent and fossil brachiopods by Shrock and Twenhofel than are given altogether to this group in the neontologic text—and this is a group about which relatively little is yet known from the ecological viewpoint.

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## The Biology of Paramecium[1]

The slipper-shaped animalcules have finally come into their own. Just two hundred and fifty years ago the first recognizable figure of *Paramecium* was drawn by an anonymous observer. Since then these tiny organisms have continued to fascinate scientists of each generation. It seems quite possible that *Paramecium* was one of the first micro-organisms to be studied by Leeuwenhoek and yet today, ultraviolet and electron microscopists continue to find these Protozoa worthy foils for their ever more intensive research.

Only a protozoologist will fully appreciate the effort and skill necessary to produce such a book as *The Biology of Paramecium*. It is certain to become a classic in its field which will stand both as a monument to biological achievement and to its author. Dr. Wichterman integrates the work of the past with that of the present so deftly that the reader is scarcely conscious of great lapses of time between observations of many workers, but the dates are given for ready reference each time an investigator is cited.

Although long known as an authority on *Paramecium bursaria*, few non-specialists may realize that for over twenty years the author has studied and cultured all of the major species of the genus *Paramecium*. Much of the author's work is presented in this book for the first time; in this and his previously published research he has employed almost every technique known to modern protozoology, and, when apparatus for a particular task did not exist, Dr. Wichterman on several occasions invented it.

Not all of the nearly 2000 papers (1919 to be exact) cited by Dr. Wichterman deal directly with *Paramecium*. However, they have been selected to broaden the reader's understanding of the ciliates, and to a lesser extent, of the Phylum Protozoa. By giving the title of each paper listed in the bibliography, Dr. Wichterman has greatly increased its usefulness to the investigator.

In this day of political bombast, which is sometimes felt even in Biology, the simple, sincere, intelligent, and constructive way in which Dr. Wichterman presents the work of others is, indeed, most refreshing. Throughout his book, almost like a refrain, one finds the author citing work on one side of a controversial issue, then evidence on the other side, and finally, his own findings; thus, the reader is given an opportunity to make his own considered judgments.

Although fifteen chapters are devoted to a

[1] **Wichterman, Ralph.** 1953. The biology of Paramecium. xvi + 527 pp. New York: Blakiston. $9.00.

review of the work done on eight major species of *Paramecium,* Dr. Wichterman consistently refrains from giving lengthy summaries of work that has been adequately discussed elsewhere. Instead, the reader is referred to the best of such sources. At times, when an exact statement is necessary for a brief appraisal of a certain aspect of *Paramecium* research, Dr. Wichterman calls on the investigator to speak for himself either through quotations from private communications or by using extensive quotations from the published work. This technique is used particularly in reviewing the extensive and thought-provoking work of Dr. Sonneborn and his school.

Except for his presentation of *Paramecium* ecology, Dr. Wichterman's book is generally well organized. The first three chapters deal with an interesting history of the genus, the classification of well-defined and uncertain species, and a scholarly review of the morphology and cytology of these ciliates. Next follows a chapter entitled, "Ecology, Collection, Cultivation, and Sterilization of *Paramecium*" which will be considered later.

A chapter on the physical and chemical properties of the protoplasm of *Paramecium* draws together much scattered information, parts of which might have been handled in the chapter on morphology and cytology. The discussion and figures devoted to microincineration and centrifugation studies are especially appropriate in such a discussion. Finally, much of the work on ultraviolet and X-radiation is reviewed, including numerous graphs, lists, and tables.

Two chapters entitled "Metabolism" together deal with the classical and newer studies on food vacuole formation with particular emphasis on Mast's work; a critical discussion of the perennial problem of the formation and function of contractile vacuoles; and, an up-to-date discussion of respiration which includes evidence for the enzymes involved, and Claff's application of the Cartesian diver technique. A section on growth in one of these chapters includes a description of Gause's work on interspecific competition. The reviewer feels this might well have been placed in another section.

Although referring to two dissimilar subjects, two chapters "Movement and Motor Response" and "Vitality Studies and the Life-Cycle" share one thing in common, both review early work which attracts scant attention today. The work of the late Dr. Jennings on taxes is the main topic of the first chapter although a short summary on trichocyst extrusion is included. Maupas, Calkins, Woodruff, and Jennings are some of the outstanding names frequently encountered in the review of the work on vitality. In the light of our present day discoveries, it is apparent that although some information from the era represented by these men may be accepted as fundamental, much of it is now seen to be inaccurate because of inadequate techniques or incomplete interpretations. In spite of the crudity of this earlier work, Dr. Wichterman's treatment of this subject leaves little doubt as to its historical significance and importance as a stimulus for contemporary research. It is interesting to note that the work of Jennings was so sound that much of it has stood the test of time. Finally, the author's comments on the replacement of the concept of endomixis by those of autogamy and hemixis are of unusual significance since he has played an important role in interpreting the scope of the last two phenomena.

Dr. Wichterman's store of knowledge and personal experience are best revealed in the two chapters entitled "Reproduction—" and "Genetics:—." Six species of the genus *Paramecium* are described in these two chapters, and the work of a host of authors is organized into an integrated whole. Most important in these discussions is the work of Sonneborn and his associates. With regard to genetics, it would seem more logical, from the standpoint of organization, to have included in this discussion Dr. Wichterman's short chapter on "Serologic Studies of *Paramecium.*" As was stated earlier, work extensively reviewed elsewhere was not covered completely by the author, however, the reviewer would have liked to have seen more space devoted to the problem of cytoplasmic inheritance with special reference to plasmagenes. Rather lost in the discussion of genetics and older regeneration studies is the significant work on morphogenesis so recently brought to the attention of American readers by Lwoff.[2]

Those not having access to the literature will value the reprinting of some of Diller's original figures on autogamy in *Paramecium aurelia* which has furnished a firm cytological background for the extensive analyses of the "aurelia" geneticists. Also valuable is Dr. Wichterman's description of the phenomenon of cytogamy, which was discovered by him and which proves that pairing of paramecia does not necessarily result in micronuclear exchange. A new emphasis is given to the work of Jollos on *Dauermodifikationen* (long lasting modification) since it can now be reconciled with recently confirmed discoveries. Finally, a review is given of the excellent work of Dr. C. B. Metz, who, using an unusual technique involving the pairing of living animals with formalin-killed ones, has thrown light on the

[2] **Lwoff, A.** 1950. Problems of morphogenesis in ciliates. New York: J. Wiley and Sons.

sequential stages of conjugation which may have further implications in an understanding of gametic syngamy.

A chapter dealing with "Organisms Living In and Upon *Paramecium*" will be of unusual interest to the ecologist. Much of the information cited is based on Dr. Wichterman's own observations. His cautious statements concerning a possible symbiotic organismal interpretation of "kappa" particles found in "killer" *Paramecium aurelia*, stock 51, are especially interesting in the light of the extensive work done with these animals. On this point, the reader is left with the feeling that only further investigation will reveal the whole story.

Since Dr. Wichterman's training and skill as a technician have been successfully demonstrated on numerous occasions, both the novice and the experienced protozoologist will be interested in testing new methods and modifications of old ones given in his chapter on techniques. Finally, in the last chapter of the book, the student will find many thought-provoking and stimulating suggestions for research on *Paramecium*.

The major weakness of this otherwise fine book, in the opinion of the reviewer, is the handling of the ecology of the paramecia. It is true that the ecologist will be both surprised and pleased to find summaries of so much material of interest to him. The chief difficulty, however, is that such information is scattered throughout the book. In Chapter 4, two pages devoted to ecology as such tell where paramecia are found and give a very brief account of the conditions under which they may exist. These two pages might well have been used as an introduction to a large chapter on ecology. The remaining part of this chapter might well have been placed in a later one which primarily deals with techniques in research. The reviewer does not wish to convey the impression that the references to ecological material are difficult to locate in this book; rather, he feels that an integrated discussion would have resulted in less repetition and provided a useful synthesis. Certainly, the two short chapters on physical and chemical stimuli as well as the one on the symbiotic relations of paramecia to other organisms should be included in a chapter on ecology. Also, Chapter 6, Section B, entitled "Growth and Factors Influencing Growth" should be included in an ecological discussion. In this section, not only are populations discussed but also such topics as allelocatalysis, acclimatization, and struggle for existence. One is pleased to find that Allee's figures on coactions are reprinted and discussed briefly; here also, the graphs, as well as a good review of Gause's work are given.

In a way, this apparent weakness in *The Biology of Paramecium* is a commentary not on Dr. Wichterman, but rather on all those biological contemporaries who still think of ecological phenomena under the specific headings of Physiology and Parasitology. The reviewer has long contended that the Protozoa hold the key to many purely population problems and that until sufficient work is done in these and other ecological fields, our colleagues will continue to ignore ecology or conceive of it only in a very limited and antiquated sense.

When it is considered that this book is a one-man effort which was sustained over a period of eight years, the next criticism is entirely understandable. At the end of many paragraphs, there are indications of "accretion," i.e., new material has been added without being wholly integrated into the context. Extensive use has been made of footnotes which contain a great deal of valuable information. The above technique, however, has resulted, in places, in a certain roughness of presentation.

The span of *Paramecium* history is effectively illustrated by the use of very old prints and copies of the most modern electron micrographs. By reprinting original figures, Dr. Wichterman has kept the flavor of the original work; however, in places, the reviewer feels that reworking of certain illustrations would have resulted in a more pleasing effect. In general, the figures are well reproduced, but in the cases of copies of old prints and some foreign illustrations the inking appears too heavy; this, however, may have been the fault of the originals.

*The Biology of Paramecium* contains remarkably few errors. Typographical errors are rare. The only factual error detected was one found in the legend of Figure 91 on page 281. Here in line five the term "pregamic" instead of "postgamic" is used.

It is apparent from the complete bibliography, list of available movies on *Paramecium*, numerous illustrations, extensive subject and author indices, and detailed table of contents that *The Biology of Paramecium* is especially designed as a reference book on the paramecia, and to a lesser extent, the ciliates. From this standpoint, some teachers may use it as a text in protozoology in the same manner that general biology is taught with a human emphasis. Regardless of the way in which it is used, this book will find a significant place among the several other outstanding ones published in the last few years on various aspects of protozoology.

Dr. Wichterman dedicated his book to the self-taught genius of Delft who personified the spirit of true research. This same spirit, passed on through generations of observers from all lands, is encountered throughout *The Biology of Paramecium*. It seems, therefore,

fitting to close this review by using a quotation selected by Dr. Wichterman from the writings of the eminent protozoologist, the late Clifford Dobell.

"Language and land and lineage are no bars to mutual and native understanding. An honest man in any country is linked to all other honest men in all other countries. When a true man like Antony van Leeuwenhoek is born, the heavens are opened. Even when he dies he is not dead: his spirit glows with the divine light forever, and will forever be seen and understood—somewhere, sometime, by somebody."

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## The Beginning of a New Era in Mexican Ornithology[1]

Our knowledge of the avifauna of Mexico has reached a stage approximately comparable to that in the United States 75 years ago. The day of the collector has nearly passed, and the vast and important phase of field observation lies ahead. Although the path has been glaringly obvious for some time, it has been blocked by the lack of a guide to the sight identification of the baffling array of nearly 1000 species, and well over 2000 races, which occur within the country. At last this hindrance has been removed by the publication of the field manual, "Birds of Mexico."

This convenient-sized volume treats every species which occurs within the boundaries of Mexico. Under each species the following data are found: its distinctive characters; its distribution within Mexico, with frequent reference to its ecological preferences; a concise list of the ranges of the races occurring within the country; and a paragraph discussing differences which serve to distinguish similar species, along with interesting bits of information on habitats, behavior, nesting, migration, etc.

Every family is illustrated by at least one line-drawing of a characteristic species; in the larger groups a number of forms are figured. Frequently these are species which do not occur north of Mexico, or are groups of related species which are difficult to identify but whose differences can be readily indicated in a black-and-white drawing. In general, the illustrations, which are by Douglass E. Tibbitts, are excellent.

The larger families are prefaced by simple keys to their species. Lacking illustrations of every species, a method of this nature must be employed, although it is far less satisfactory than the elaborate color plates to which we are accustomed in manuals on the birds of the United States.

Through no fault of the author, the keys are not completely satisfactory. Often the differences between several species are so slight it has been necessary to resort to very minor size- or color-differences in order to distinguish them. Many of these characters can be observed only under the most favorable conditions, and thus are not of general use. Also, concise descriptions of minor variations are not easy to visualize, although usually a simple color plate can readily convey the differences. It is regrettable that the single plate in this volume is a garish and poor representation of the virtually unmistakable Collared Araçari. It would have been much more useful if it had been used for a group of hard-to-identify flycatchers, or another difficult complex. It is hoped, however, that the book will meet with a heavy demand, which it so justly deserves, and that the publishers will find it economically feasible to include more plates in later editions.

Even though it must be admitted frankly that this book is not in a class with the American guides, one must take cognizance of the fact that it covers a vastly larger avifauna and that it is a trail-blazer. Appreciating this, it may be said that Blake has had the enviable opportunity of opening up what will undoubtedly be a vigorous new phase of Mexican ornithology, and he has done it well.

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[1] **Blake, Emmet Reid.** 1953. Birds of Mexico. A Guide for Field Identification. xxix + 644 pp., 1 color pl., 329 line-drawings. Chicago: University of Chicago Press. $6.00.

## The Immaculate Forest[1]

Dr. Philipson gives an interesting and straightforward account, on a popular level, of a biological expedition into the jungle. A few of his passages would profit by some revision, but his occasional lapses do not seriously detract from the rest of the book. In the first chapter he skips from one time and place to another with so little transition as to produce some confusion. This, compounded with the subtitle referring to the book as "An account of an expedition to the unexplored territory between the Andes and the Amazon," makes it easy for the reader to miss the fact that the Macarena mountains are well within the southwestern drainage of the Orinoco, rather than in that of the Amazon. The last chapter on the reasons for biological exploration in the area are adequate for those familiar with the distributional and evolutionary problems presented by the high isolated mountains of northern South America. It seems, however, that the inclusion of somewhat more detailed background material would be of benefit to many others who will no doubt read the book.

The author has, in most cases, avoided the overgeneralization and exaggeration found in many popular accounts of the tropics. The most striking lapse in this respect is a conclusion he reaches relating to a slow-moving column of caterpillars, moving two or three abreast in a sinuous band several feet long. He says that these caterpillars are "thought to be an example of defenseless creatures passing themselves off as a dangerous one, and so keeping insectivorous birds at a safe distance."

Dr. Philipson shows that an expedition into the jungle, apparently believed by many to be a carefree adventure, involves a staggering amount of hard, messy work. The results can, however, be most rewarding.

He gives many descriptions of various parts of the jungle, drawing a very profitable parallel between the inner jungle and the temperate deciduous forests in respect to density of undergrowth. The book will be of value to those wishing a lucid, generally accurate and easily read account of an expedition into the jungle.

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[1] **Philipson, W. R.** 1952. The immaculate forest. 223 pp., 32 photographs, 2 maps. New York: Philosophical Library. $4.50.

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